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Ten Species of *Pisione* (Annelida: Polychaeta: Pisionidae) from Japan and Evolutionary Trends in the Genus Based on Comparison of Male Copulatory Apparatus

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Abstract Five new species and three new subspecies of the genus *Pisione* are described based on material from Japan. In addition, *P. parva*, newly recorded from Japan, and *P. africana*, once recorded from Japan without description, are described. Results of SEM observations, especially on their male copulatory apparatus, are presented. Japanese fauna with as many as 14 species is summarized. Male copulatory apparatus in the whole genus are compared, and four groups of closely related species are recognized. Their phylogenetic relationships and evolutionary trends are discussed.

Key words: *Pisione*, Polychaeta, copulatory apparatus, SEM observations

Introduction

The family Pisionidae is a group of small, agile polychaetes living in marine sandy sediment. It comprises four genera, *Pisione* Grube, 1857 with 28 species and one subspecies, *Pisionella* Hartman, 1939 with a single species, *Pisionidens* Aiyar and Alikunhi, 1943 with three species, and *Anoplopisone* Laubier, 1967 with two species.

Genus *Pisione*, with so many species, is widely distributed in the world. Five species, *P. longipalpa*, *P. crassa*, *P. papillata*, *P. africana* and *P. subulata* have so far been recorded from Japanese waters (Uschakov, 1956; Yamanishi, 1976 and 1992; Uchida, 1988) though morphological description has not yet been given for *P. africana*. In the course of the recent research on the interstitial polychaete fauna along Japanese coasts, the author could obtain material of ten species of *Pisione*, all of which except for *P. africana* are new to the Japanese fauna. They are examined in detail using SEM; special attention is paid on their male copulatory apparatus.

This paper presents the description of the ten species with a summary of the Japanese fauna, and at the same time, a phylogenetic consideration in the genus based on the comparative analyses of the male copulatory apparatus is attempted.

Methods

Collection and Extraction:

Most of the samples were collected at marine sandy beaches of various localities along Japanese coasts by scooping several liters of wet sediment around the water's edge at low tides. At Futami Bay, Chichi-jima, Bonin Islands, sediment of shallow sandy bottom was obtained by dredging from shipboard. Subtidal sand among rocks and corals was sampled by SCUBA-diving at Amitori Bay, Iriomote Island, Okinawa Prefecture.

Meiofaunas were extracted from those sediment samples by repeated (usually four times) stirring and decantation in sea water using a receiving net made of gauze for plankton net (NXX-16) after fixed by 1/10 formalin (Yamanishi, 1979). Worms sorted out were transferred into 70% ethanol.

Observations:

The entire bodies of the worms were photographed under an equipment for photomacrography

(Nikon's MULTIPHOT) through transmitted light, except for an extraordinarily large species which was taken by a camera using a close-up lens under reflected light.

Observations and drawings of the worms were made under a light microscope of up to 1,000 total magnification; microphotographs were taken simultaneously, and the developed films were projected to a screen where outlines as the bases for the detailed drawings were traced beforehand.

Several specimens of each species were offered for the observation under scanning electron microscopy (SEM). For preparation, they were critically dried in carbon dioxide, and were coated with platinum-palladium using an ion sputter. Observations were made and photographs were taken under the SEM of HITACHI's S-501 type.

Depositary:

Materials examined in the present study were deposited in the Osaka Museum of Natural History. The registration numbers are prefixed by "OMNH-IV".

Systematic Accounts

Family Pisionidae Southern, 1914

All the species of the family are elongated worms with numerous setigerous segments (=setigers). The prostomium is more or less reduced, surrounded by the succeeding, enlarged segment (= buccal segment). Prostomial antennae are absent except for *Pisionella* which is provided with a dorsal, median one. The buccal segment is asetigerous though provided with a pair of unique buccal acicula in *Pisione* and *Anoplopisione*. The segment bears two pairs of (dorsal and ventral) cirri; the dorsal cirri are tentacular and direct forward in every genus, while the ventral ones are tentacular (in *Pisionella*), flask-shaped (in *Pisione* and *Anoplopisione*), or absent (in *Pisionidens*). Paired palpi, each supported by a thick sheath, arise from below the buccal segment and extend anteriorly beyond the dorsal cirri of the buccal segment. Below and behind the sheath of palpi opens anteriorly the mouth from which protrudes a muscular, retractile proboscis. The parapodia of body segments are sub-biramous and are provided each with a dorsal and a ventral cirri both of which are usually flask-shaped. The notopodium of parapodium is reduced and fused to the neuropodium; it is represented only by an aciculum (notoaciculum). The parapodial stem of the neuropodium is well-developed with a bundle of setae and an aciculum (neuroaciculum). In *Anoplopisione*, parapodia of 2nd segment are devoid of setae. In adults of *Pisionidens*, all the segments are uniramous and asetigerous; however, the juveniles are known to possess neuropodial stem with a bundle of setae and two acicula on some anterior segments. In *Pisione* and *Pisionidens*, prominent male copulatory devices which are composed of a bulge of gonadal pore and modified parapodial elements are developed on some body segments.

Genus *Pisione* Grube, 1857

Diagnosis:

Prostomium reduced and surrounded by buccal segment, without antennae. Dorsal cirri of buccal segment tentacular. Ventral cirri of buccal segment flask-shaped. Buccal acicula present in most species. Body segments setigerous. Dorsal and ventral cirri of parapodia of body segments uniformly flask-shaped except for ventral ones of 1st setiger and dorsal ones of 2nd setiger being elongated or tentacular. Single or bilobed

presetal lobes well-developed. Two acicula embedded in a parapodium; notoacicula, usually smaller than neuroacicula, enlarge and project through the skin in some species. Four types of setae, supra-acicular simple setae, infra-acicular simple setae, long-bladed compound setae, and falcigers present. Pygidium with a pair of anal cirri. Male copulatory apparatus of diverse features.

General Account:

Trunk is dorsally flattened and ventrally swollen. The prostomium (Fig. 1A: 1) is reduced and surrounded by the buccal segment; the border is distinct or indistinct. The anterior seam of the buccal segment is usually visible as a median groove. Prostomial antennae are absent. Paired eyes are situated on one of the anterior setigers, occasionally accompanied by an additional pair more posteriorly. Brain (Fig. 1A: 2) starts from just behind the prostomium and extends backward into some anterior segments; it is bilobed posteriorly. The buccal segment (Fig. 1A: 3) is enlarged so much as to occupy the main cephalic region. It is asetigerous and bears two pairs of cirri: the dorsal ones (Fig. 1A: 4) are tentacular and direct forward; the ventral ones (Fig. 1A: 5) are small and globose, suspended at the basal part of the former. A pair of buccal acicula (Fig. 1A: 6) is present; they converge forwards and, in most species, project through the skin; their distal ends are expanded. The palpi (Fig. 1A: 7) are long and powerful, each supported basally by a thick sheath. The mouth is ventrally supported by a lip. The pharynx lies extending over several anterior setigers when retracted. It is provided with numerous terminal papillae and four chitinous jaws (Fig. 1A: 10). The anterior part of the jaw is thickly chitinized; its inner side is supported by a membranous structure; an acute inward projection may be present subterminally.

Body segments following the buccal segment are setigerous and basically uniform throughout the body. The dorsal and ventral cirri of parapodia are small and flask-shaped provided with some palpocils. The dorsal cirrus (Fig. 1B: 12) attaches to the dorsum just above the base of the parapodial stem; the ventral cirrus (Fig. 1B: 13) is suspended at the lower margin of the parapodial stem; they are equal in size throughout except for the ventral ones of 1st setiger and the dorsal ones of 2nd setiger: the former (Fig. 1A: 8) are always more or less elongated and tentacular, projecting forward with their bases shifted inwards near the frontal base of the parapodia; the latter (Fig. 1A: 9) may be elongated projecting laterally, or small and flask-shaped. The notoacicula (Fig. 1B: 14) are straight and weak, though in some species they grow strongly and project through the dorsal wall of parapodia; the neuroacicula (Fig. 1B: 15) are thick with their distal ends usually curving ventrally. The distal part of parapodial stem is characterized by a well-developed presetal lobe; it is either bilobed with the superior and the inferior lobules (Fig. 1B: 11), or single with the inferior lobule reduced; in some species, they are bilobed in anterior segments and become single posteriorly; "terminal pores" (Plate IV: 5) of presumably adhesive function are distributed on the surface of the superior lobules.

All the bundles of setae comprise at least two kinds: one simple seta from supra-acicular position (=superior to the neuroaciculum, Fig. 1B: 16) and several compound setae with falcate blades (=falcigers) from infra-acicular position (=inferior to the neuroaciculum, Fig. 1B: 19). The former is thick and the distal part is obliquely truncate with serration along the edge. The blade of the latter is coarsely serrated; the distal end of the shaft is bifurcate, followed by a distinct subterminal notch. In addition, long-bladed compound setae (Fig. 1B: 17) and infra-acicular simple setae (Fig. 1B: 18) may be present. The former usually arises singly from the infra-acicular position, superior to the falcigers; the blade, provided with fine serration, is distinctly longer and more slender than those of the

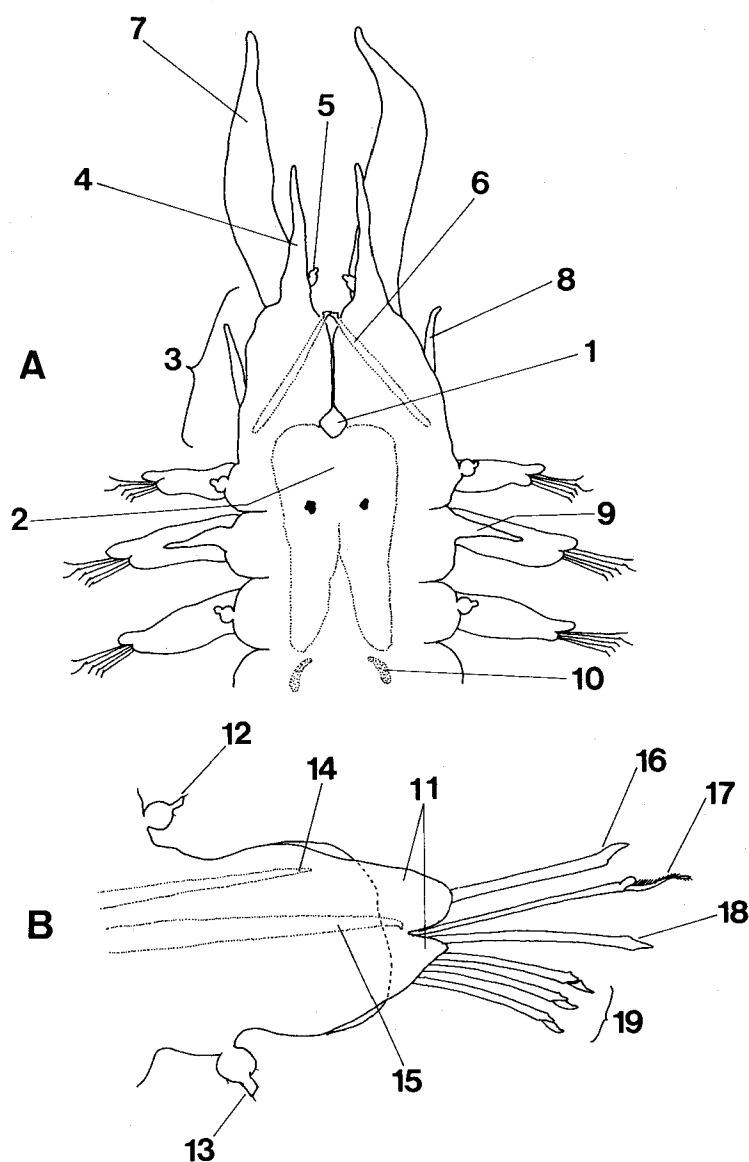


Fig. 1. Schematic presentation of anterior end and parapodium of *Pisone*. A. Dorsal view of anterior end; B. Anterior view of a parapodium. 1: prostomium, 2: brain, 3: buccal segment, 4: dorsal cirrus of buccal segment, 5: ventral cirrus of buccal segment, 6: buccal aciculum, 7: palp, 8: ventral cirrus of 1st setiger, 9: dorsal cirrus of 2nd setiger, 10: jaw, 11: presetal lobe, 12: dorsal cirrus, 13: ventral cirrus, 14: notoaciculum, 15: neuroaciculum, 16: supra-acicular simple seta, 17: long-bladed compound seta, 18: infra-acicular simple seta, 19: falcigers.

falcigers, and usually twists terminally; its shaft is thinner than those of the falcigers and the distal end is usually peculiar with a broad extension covering the basal part of the blade anteriorly (= anterior distal plate). The latter is usually thick and acicular, with or without serration, variable in size and shape.

Fertilization in the genus is achieved through true copulation. On some setigers of mature males, copulatory organ as a bulge of gonadal pore arises ventrally from the base of the parapodial stem and extends laterally accompanied by various secondary appendages. The ventral cirrus there may either enlarge and modify itself or otherwise diminish. The parapodial stem may remain unmodified or be fused to the copulatory organ with varying degrees; the setae may be intact, partly reduced, or absent; the flask-shaped dorsal cirrus always remains unmodified. In females, such complicated copulatory devices are not recognized; in some species, genital papillae are known to be situated ventrally at the base of parapodia of fertile segments.

The pygidium is asetigerous; a pair of anal cirri is attached to the posterior extremity. The caudal glands of presumably adhesive function may develop on the pygidium (Plate V: 7,8).

Pisione africana Day, 1963

Pisione africana Day, 1963: 390–391

P. africana: Hartmann-Schröder, 1970: 55–57; Uchida, 1988: 85

P. crassa: partly in Yamanishi, 1976: 375, Fig. 2a

Material. Ten male and three sexually undetermined specimens were collected from the lower intertidal zone of a sheltered, very coarse sand beach near Haimizaki, southeastern coast of Iriomote Island, Taketomi-cho, Yaeyama Islands (24°15'00"N, 123°52'40"E), subtropical archipelago of southwestern Japan, on April 16th 1995. Specimens are deposited as shown in Table 1.

Diagnosis: Body length up to 20.4 mm with more than 100 setigers. Prostomium distinct. Buccal segment characteristic of the genus. Jaws without inward projection. Ventral cirri of 1st setiger even longer than the dorsal cirri of the buccal segment. Dorsal cirri of 2nd setiger elongated. Presetal lobes bilobed throughout the body. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal

Table 1. Body size, and position of male copulatory apparatus and infra-acicular simple setae in *Pisione africana* Day, 1963.

Sex	Body length (mm)	Number of setigers	Copulatory apparatus	Infra-acicular simple setae	Registr. No. (Iv)	Remarks
male	16.4	108	25–50th	7–17th; 7–17th	1355	
male	20.4	129	24–69th	7–18th; 7–20th	1356	
male	13.2	104	27–48th	absent	1357	
male	15.1	103	25–44(?)th	9–17th; 9–15th	1358	
male	19.3	137	24–69th	present	1359	
male	13.3	107	29–53th	9–13th; 8–12th	1360	
male	?	?	present	?	1361	
male	9.7	73	25–47th	absent	1362	
male	?	?	present	?	1363	
male	16.1	104	24–49th	?	1364	SEM
?	12.2	89	absent	absent	1365	
?	17.9	118	absent	absent	1366	
?	18.8	112	absent	absent	1367	

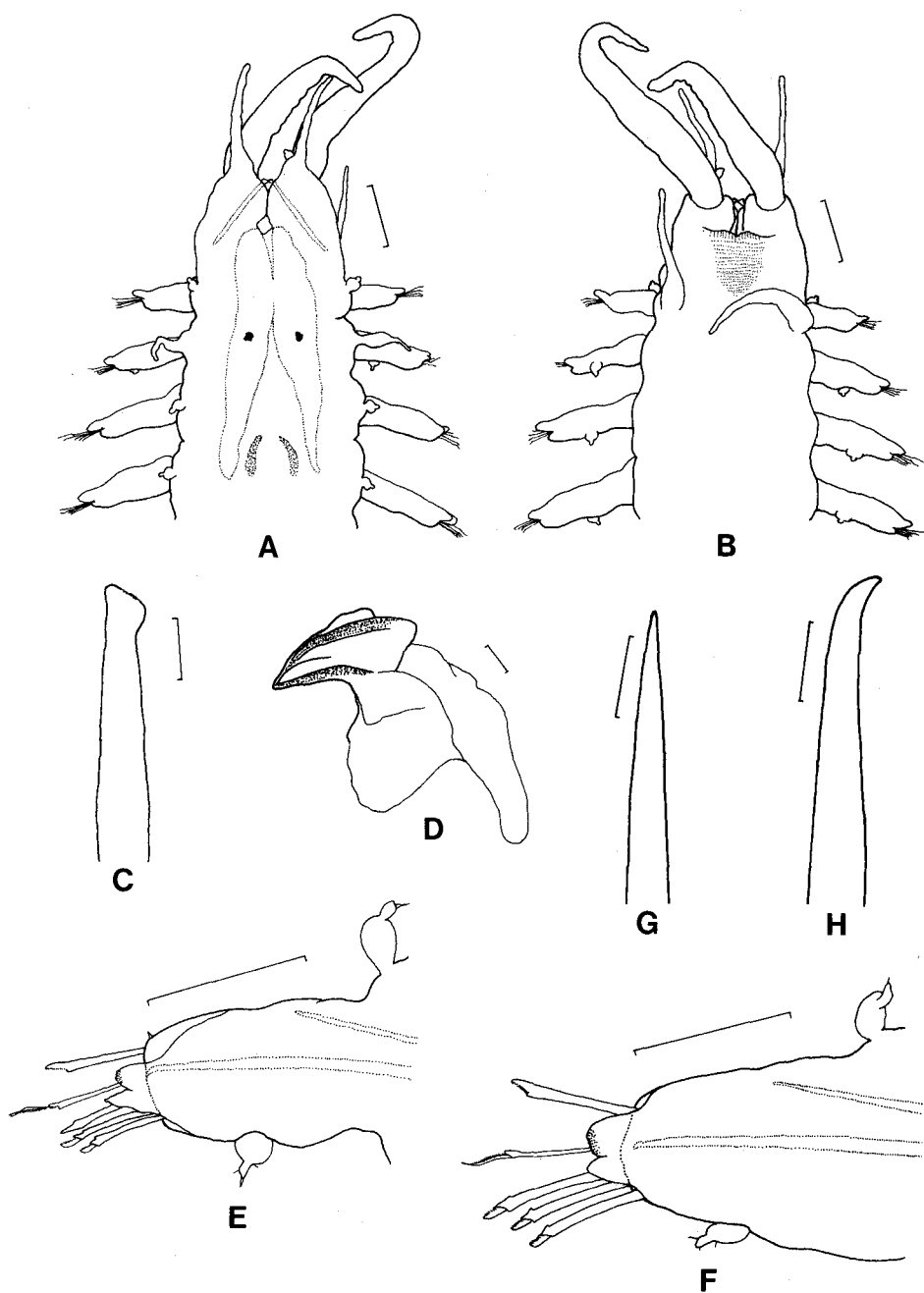


Fig. 2. *Pisione africana* Day, 1963. Male, Iv 1355. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (7th setiger); F. Anterior view of a median parapodium (52nd setiger); G. Notoaciculum (59th setiger); H. Neuroaciculum (59th setiger). Scale. A, B, E, F: 0.1 mm; C, D, G, H: 0.01 mm.

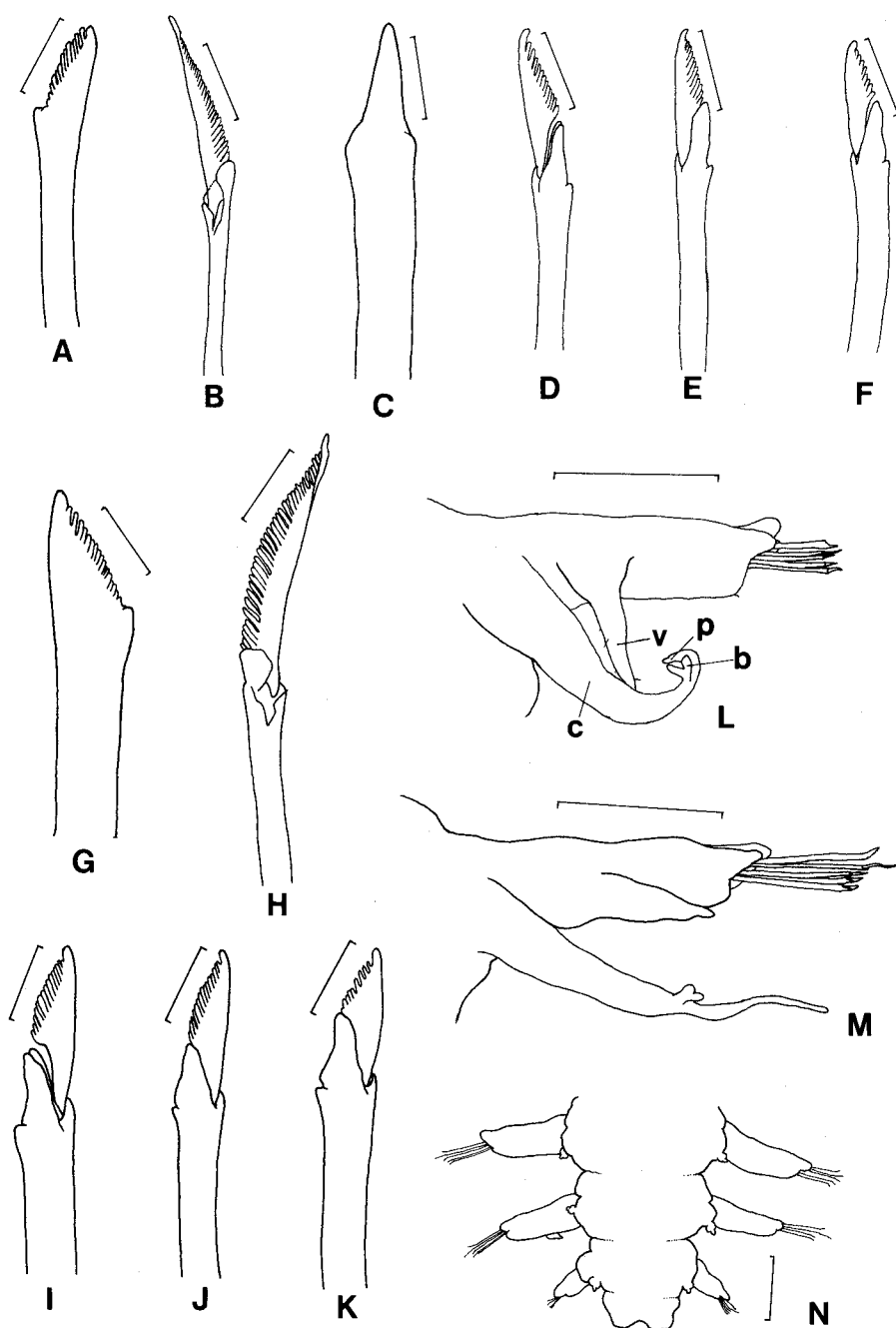


Fig. 3. *Pisione africana* Day, 1963. Male, Iv 1355. A. Supra-acicular simple seta (5th setiger); B. Long-bladed compound seta (5th setiger); C. Infra-acicular simple seta (7th setiger); D-F. Falcigers (5th setiger) from upper to lower; G. Supra-acicular simple seta (59th setiger); H. Long-bladed compound seta (59th setiger); I-K. Falcigers (59th setiger) from upper to lower; L. Posterior view of a copulatory organ together with elongated ventral cirrus (33rd setiger); M. Posterior view of an incomplete copulatory organ with slender distal end, ventral cirrus not fully elongated (49th setiger); N. Dorsal view of posterior end (anal cirri detached). b: bidigitate process, c: copulatory organ proper, p: penis, v: ventral cirrus. Scale. A-K: 0.01 mm; L-N: 0.1 mm.

plate and three falcigers on every parapodium; an infra-acicular simple seta may replace the uppermost falciger on some anterior segments in males. Male copulatory apparatus prevailing on numerous consecutive segments; parapodial stems and setae of these segments unmodified, while ventral cirrus elongated; copulatory organ proper elongated, ending in a cuticular process provided subterminally with a bidigitate process.

Habitus (Plate I: 1):

The body attains a length of 20.4 mm and the number of setigers amounts to 137 (Table 1). The shape of the entire worm is slender; the trunk gradually tapers posteriorly. The segments provided with male copulatory apparatus are not conspicuous when observed under low magnification. The trunk is usually about 0.3 mm in width exclusive of parapodia; the lengths of the parapodial stems of 1st setiger are 0.08 mm; the stems abruptly enlarge at 2nd setiger with lengths of 0.15 mm and attain the average length of 0.17–0.18 mm after 5th setiger.

Colour:

White in alcohol.

Anterior end (Fig. 2A, B; Plate II: 1, 2):

The prostomium is diamond-shaped. The brain extends back to the position of about 4th setiger. One pair of eyes is located at the position of about 2nd setiger. The buccal segment slightly tapers anteriorly; the dorsal cirri are 0.17 mm long; the ventral cirri are small and flask-shaped. The buccal acicula are well developed with lengths of about 0.15 mm; they project through the skin anteriorly; their distal ends are expanded (Fig. 2C). The palpi are 0.39 mm long in a specimen (Iv 1355). The pharynx extends over around 4–9th setigers. The jaws are devoid of inward projection (Fig. 2D).

Parapodia (Fig. 2E, F; Plate IV: 1):

The ventral cirri of 1st setiger are longer than the dorsal cirri of the buccal segment. The dorsal cirri of 2nd setiger are obviously elongated though not exceeding the parapodial stem of the same segment. The presetal lobes are bilobed throughout the body. In the anterior segments, the inferior lobules are longer than the superior ones; this relation in size is reversed in the median and the posterior segments. The terminal pores are numerous on the superior lobules. The notoacicula are straight (Fig. 2G) and never project through the body wall. The neuroacicula curve ventrally at the tip (Fig. 2H).

Setae (Fig. 3A-K; Plate VI: 1–6):

There are usually one supra-acicular simple seta, one long-bladed compound seta and three falcigers on a parapodium. An infra-acicular simple seta may replace the uppermost falciger at least in males (Table 1); when the infra-acicular simple setae are present, they appear on some of the anterior segments consecutively, starting from 7–9th setiger. The distal part of the supra-acicular simple setae is obliquely truncate and serrated with about 15 teeth along the edge. The infra-acicular simple setae are smooth with a subterminal notch at one side and with a gradual oblique expansion forming a blunt angle more proximally at the opposite side. The blade of the long-bladed compound setae is finely serrated with more than 30 teeth; the distal end of the shaft stretches obliquely towards the cutting side of the blade forming the anterior distal plate, and turns to the opposite side partly covering the basal part of the blade. The upper and the middle falcigers are provided with about 15 teeth on a blade while the lower with 8–9 teeth.

Copulatory apparatus (Fig. 3L, M.; Plate IX: 1, 2):

The male copulatory apparatus are arranged consecutively on many segments which start from 24–29th and reach 47–69th setiger (Table 1). The ventral cirri of these segments are enlarged as thick, tapering processes with many palpocils; the cirri project laterally in front of the copulatory organ proper not exceeding the end of the parapodial stem. The parapodial stem, the setae and the dorsal cirri remain unmodified. The copulatory organ proper arises as a thick process from the base of the parapodial stem ventro-laterally, and reaches as long as the parapodial stem; it tapers terminally ending in a recurved, cuticularized penis; in addition, a bidigitate process arises subterminally. Incomplete penes are observed on some segments in a specimen (Iv 1355); they are cirriform and not cuticularized.

Posterior end (Fig. 3N):

The pygidium tapers posteriorly, with a pair of anal cirri, though not drawn in the figure.

Remarks

The present species is characteristic in the elongation of the dorsal cirri of 2nd setiger and in the possession of the bilobed presetal lobes throughout the body. Species sharing both of these characters other than *P. africana* are limited to *P. papillata* Yamanishi, 1976, *P. tortuosa* Hartmann-Schröder & Parker, 1990 and *P. ungulata* De Wilde & Govaere, 1995. The male copulatory apparatus of the present material is very similar to that of the holotype of *P. africana* which was reexamined by Hartmann-Schröder (1970). The subterminal process, however, is “ein kleiner cirrenförmiger Fortsatz” in the holotype whereas it is a bidigitate process in the present material. This difference might be attributed to the immature condition of the organ in the holotype. In other respects the present material is well referable to *P. africana*. The present species entirely differs from *P. papillata* whose male copulatory organ bears a distinct spinous papillae and lacks setae. *P. tortuosa* is an invalid species as is shown in the discussion of the present paper. *P. ungulata* should be closely related to the present species, since the basic structure and the location of male copulatory apparatus are common to them; they can be distinguished only by the shape of the parapodial cirri which are cylindrical to leaf-shaped, and by the notoacacula which project through body wall, in the former.

The maximal body length and number of setigers in the present material exceed those of the holotype (15 mm long with 75 segments).

In the original description of *P. crassa*, the author presented a figure of its male copulatory apparatus (Yamanishi, 1976: 375, Fig. 2a). Recently he observed the apparatus on newly obtained material using SEM, and revealed that it is more complicated than that drawn in the original description, pointing out that “the intricate structure of the copulatory organ together with its appendages was overlooked” (Yamanishi, 1991: 3). The apparatus of the holotype was also reexamined through light microscope and the situation was also confirmed there. At present, however, the author can ashamedly conclude that the material of the copulatory apparatus observed in the original description was not that of *P. crassa*, but of *P. africana* which is assumed to have been mixed into the material by careless treatments, because the figure drawn there is no doubt identical with that of *P. africana* presented here.

Pisone parva De Wilde & Govaere, 1995

Material. Three males and one female were collected from the sandy bottom of 10–13 m deep in Futami Bay, Chichi-jima, Bonin Islands, Ogasawara, Tokyo (27°04'40"N, 142°12'22"E), isolated

subtropical islands of southern Japan, on January 14th, 1995. One of the males (Iv 1369) and the female (Iv 1370) are immersed. Other males (Iv 1371–1372) are prepared for SEM observation.

Diagnosis: Minute species with body length up to 3.0 mm (holotype) with less than 30 setigers. Prostomium and anterior median groove invisible. Buccal segment characteristic of the genus. Jaws with an inward projection. Ventral cirri of 1st setiger short, only slightly longer than those of other segments. Dorsal cirri of 2nd setiger small, flask-shaped. One obliquely truncate supra-acicular simple seta and three falcigers on a parapodium. A few pairs of male copulatory apparatus located separately; parapodial stem and copulatory organ proper fused to each other; setae and ventral cirri absent; a hood ornamented with papillae present.

Habitus (Plate I: 2, 3): The male (Iv 1369) is 1.7 mm long and 0.16 mm wide with 17 setigers; the female (Iv 1370) is 2.5 mm long and 0.17 mm wide with 26 setigers. The width of the trunk is subequal throughout the body. The parapodial stem of 1st setiger is 0.06 mm long; it abruptly enlarges at 2nd setiger into 0.1 mm long; on the median segments it attains lengths of around 0.15 mm. The segments provided with male copulatory apparatus are conspicuously expanded laterally. Sporadically arranged gonadal segments of the female are also visible through transmitted light.

Colour:

White in alcohol.

Anterior end (Fig. 4A, B; Plate II: 3, 4):

Both the prostomium and the anterior median groove are invisible. The brain extends back to the position of 4th setiger. A pair of eyes is located on the position of 3rd setiger. The buccal segment tapers anteriorly; the dorsal cirri are 0.07–0.08 mm long; the ventral cirri are minute, globose structures. The buccal acicula are well-developed with lengths of 0.07 mm in the male (Iv 1369) projecting through the skin anteriorly; they are expanded terminally and pointed at both angles (Fig. 4C). The palpi are 0.23–0.25 mm long. The pharynx extends over 5–7th setigers. The jaws are equipped with an inward projection (Fig. 4D).

Parapodia (Fig. 4E, F; Plate IV: 2):

The ventral cirri of 1st setiger are short and only slightly longer than those of other segments. The dorsal cirri of 2nd setiger have the same shape and size as those of the following segments. The presetal lobes are bilobed nearly throughout the body in the male (Iv 1369), while they become single posteriorly in the female (Iv 1370); the superior lobule is round with a small number of terminal pores; the inferior lobule is short, and triangular or terminally pointed.

The notoacicula are straight, while the neuroacicula curve ventrally at the tip (Fig. 4G).

Setae (Fig. 4H–N; Plate VI: 7–10):

There are one supra-acicular simple seta and three falcigers on a parapodium. The distal part of the simple setae is obliquely truncate and serrated with 13–19 teeth along the edge. The falcigers have 11–12 teeth on a blade.

Copulatory apparatus (Fig. 4O; Plate IX: 3–5):

In the male (Iv 1369), two pairs of copulatory apparatus are located on 11th and 16th setigers. The parapodial stems of these segments are fused to the copulatory organ;

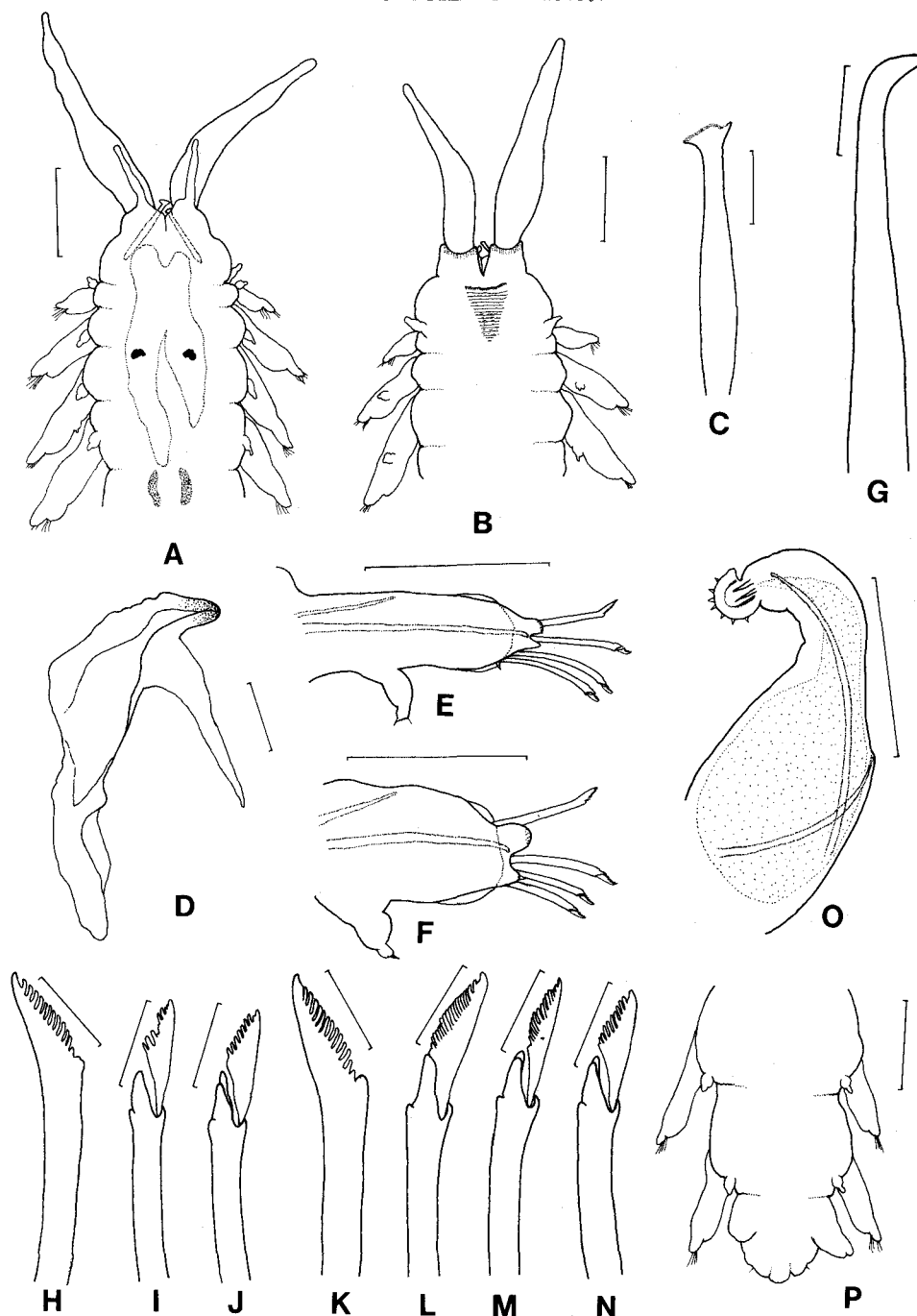


Fig. 4. *Pisione parva* De Wilde & Govaere, 1995. A-N: Iv 1369. Male; P: Iv 1370. Female. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (5th setiger); F. Anterior view of a median parapodium (14th setiger); G. Neuroaciculum (14th setiger); H. Supra-acicular simple seta (5th setiger); I. Median falciger (5th setiger); J. Lower falciger (5th setiger); K. Supra-acicular simple seta (14th setiger); L-N. Falcigers (14th setiger) from upper to lower; O. Copulatory organ (16th setiger); P. Dorsal view of posterior end (anal cirri detached). Scale. A, B, E, F, O, P: 0.1 mm; C, D, G-N: 0.01 mm.

two acicula are embedded; the dorsal cirri remain unmodified while the ventral cirri are not recognized. The copulatory organ is nearly as long as the parapodial stems of other sterile segments, extending postero-ventrally with a basal expansion where the sperm sac is involved. The terminal part of the organ recurves anteriorly forming a hood ornamented with spines. The hood is presumed to surround the retractile penis.

Posterior end (Fig. 4P):

The female specimen is observed to bear the pygidium which tapers posteriorly; it is not visible in the male (Iv 1369), probably torn off by accident. Both specimens lack the anal cirri.

Remarks

The present material well agrees with *P. parva* De Wilde & Govaere, 1995 in size, the reduced condition of the cephalic appendages, the shape of parapodia, the arrangement of the setae, and the structure and the location of male copulatory apparatus. Not any characters separating them can be recognized.

The copulatory apparatus of the present species is related to that of *P. gopalai* (Alikunhi, 1941) and of *P. paucisetosa* sp. nov. in the fusion of the parapodial stem to copulatory organ, in the lack of the setae and the ventral cirrus, and in the hood formation. The apparatus of the present species is distinguished from those of the two species in the elongated shape, and in the absence of spinous papillae and fan-like appendage.

Pisone brevicirra platycauda subsp. nov.

Material. Five male and one sexually undetermined specimens were collected from the subtidal sandy bottom of 5 m deep near the mouth of Amitori Bay, northwestern part of Iriomote Island, Taketomi-cho, Yaeyama Islands (24°17'46"N, 123°40'11"E), subtropical archipelago of southwestern Japan, on April 23rd, 1995. Type series is designated as shown in Table 2.

Diagnosis: Body length up to 4.2 mm. Prostomium obscure. Buccal segment characteristic of the genus. Ventral cirri of 1st setiger short, only slightly longer than those of other segments. Dorsal cirri of 2nd setiger small, flask-shaped. Presetal lobes bilobed throughout. One obliquely truncate supra-acicular simple seta and three falcigers on anterior segments; from about 8th setiger, the uppermost falciger replaced by an infra-acicular simple seta. A single pair of male copulatory apparatus on a median segment; their parapodial

Table 2. Body size and position of male copulatory apparatus in *Pisone brevicirra platycauda* subsp. nov.

Sex	Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
male	3.0	30	19th	1373	holotype
male	3.8	38	19th	1374	paratype
male	3.5	42	20th	1375	paratype
?	2.6	25	absent	1376	paratype
male	4.2	43	19th	1377	paratype, SEM
male	?	?	present	1378	paratype, SEM

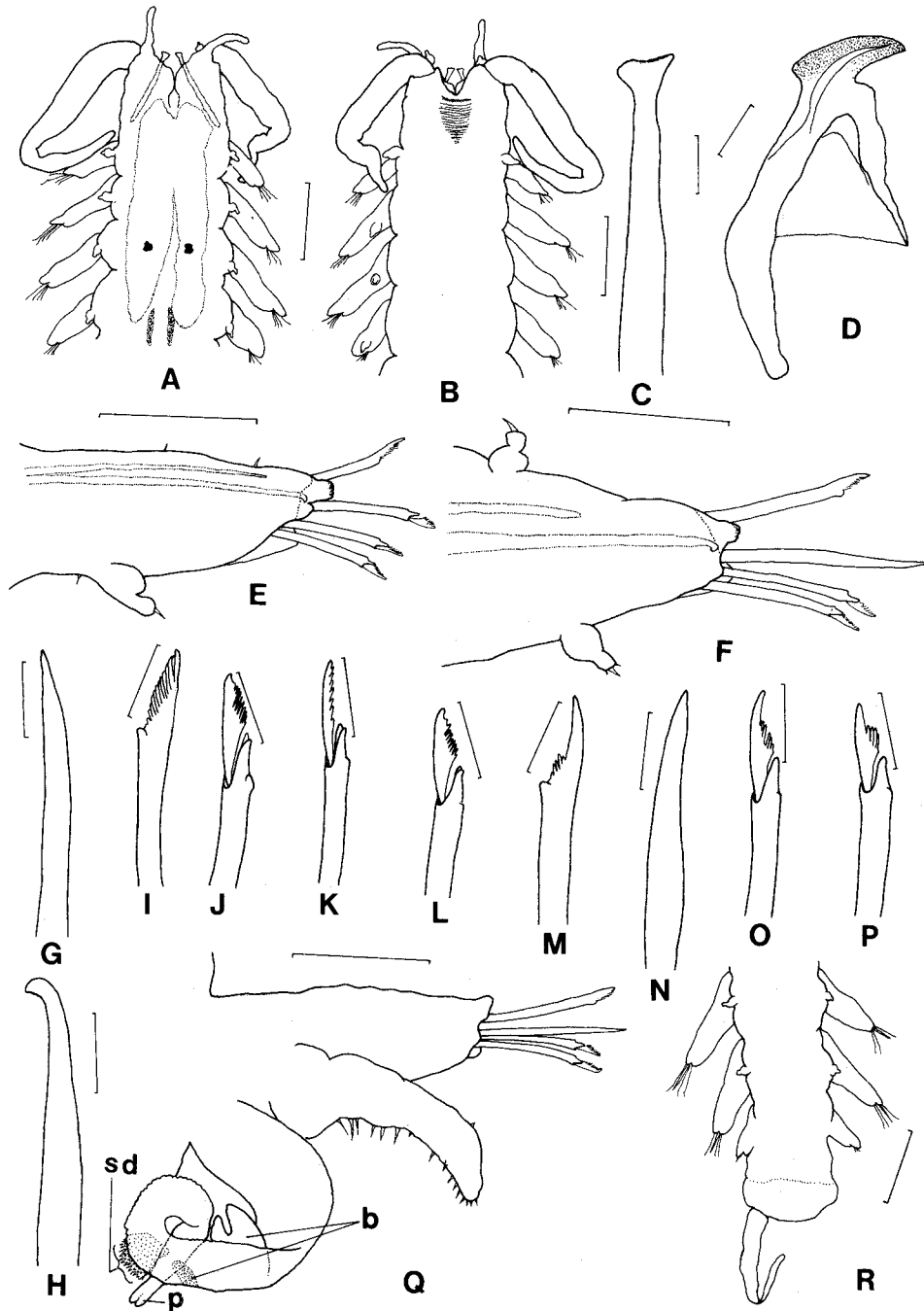


Fig. 5. *Pisione brevicirris platycauda* subsp. nov. Holotype, Iv 1373. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (4th setiger); F. Anterior view of a median parapodium (25th setiger); G. Notoaciculum (22nd setiger); H. Neuroaciculum (22nd setiger); I. Supra-acicular simple seta (4th setiger); J-L. Falcigers (4th setiger) from upper to lower; M. Supra-acicular simple seta (22nd setiger); N. Infra-acicular simple seta (22nd setiger); O-P. Falcigers (22nd setiger) from upper to lower; Q. Anterior view of a copulatory organ (19th setiger); R. Dorsal view of posterior end. b: bidigitate process; p: penis; sd: spinous pad. Scale. A, B, E, F, Q, R: 0.1 mm; C, D, G-P: 0.01 mm.

stem and setae unmodified; ventral cirri elongated. Copulatory organ forming a spiral accompanied by a spinous pad and a small bidigitate process terminally and a larger bidigitate process more basally. Pygidium semi-circular.

Holotype:

Male. Body length 3.0 mm with 30 setigers. Width of trunk, exclusive of parapodia, 0.16 mm at 7–8th setigers. Parapodial stems nearly as long as the width of the same segment except for some anterior ones; those of 1st setiger 0.10 mm long where the trunk being 0.14 mm wide. Brain extending back to the position of 4th setiger. Paired eyes located at the position of 3rd setiger. Dorsal cirri of buccal segment 0.06 mm long; buccal acicula 0.11 mm long; palpi 0.40 mm long; pharynx extending over 4–7th setigers. Ventral cirri of 1st setiger 0.03 mm long. Infra-acicular simple setae from 8th setiger on. Copulatory apparatus on 19th setiger.

Habitus (Plate I: 4):

The largest specimen attains a body length of 4.2 mm with 43 setigers (Table 2). The entire worm is short and rather thick, only slightly tapering posteriorly. A single pair of male copulatory apparatus is visible under low magnification on a middle segment. The parapodial stems are nearly as long as the width of the same segment except for some anterior ones which are much smaller. The pygidium is conspicuous by its flattened, semi-circular appearance.

Colour:

White in alcohol.

Anterior end (Fig. 5A, B; Plate II: 5, 6):

The prostomium is rather obscure; the anterior median groove is very short. The brain extends back to the position of about 4th setiger. A pair of eyes is located at the position of about 3rd setiger. The lateral margins of the buccal segment are parallel to each other not tapering anteriorly; the dorsal cirri are short; the ventral cirri are small, flask-shaped. The buccal acicula are well developed projecting through the skin anteriorly; their distal ends are expanded and truncate (Fig. 5C). The palpi are thick and long. The pharynx extends over around 4–7th setigers. The jaws are equipped with an inward projection (Fig. 5D).

Parapodia (Fig. 5E, F; Plate IV: 3):

The ventral cirri of 1st setiger are short, only slightly longer than those of other segments. The dorsal cirri of 2nd setiger have the same shape and size as those of the following segments. The presetal lobes are bilobed throughout the body; the superior lobes are always longer than the inferior ones; the terminal pores are bore on the superior lobes.

The notoacacula are straight (Fig. 5G), while the neuroacacula acutely recurve ventrally at the tip (Fig. 5H).

Setae (Fig. 5I-P; Plate VI: 11–14):

In the anterior segments, there are one supra-acicular simple seta and three falcigers on a parapodium. From around 8th setiger on, the uppermost falciger is replaced by an infra-acicular setae. The distal part of the supra-acicular simple seta is obliquely truncate and coarsely serrated along the edge. The infra-acicular simple seta is thick and acutely pointed terminally; it lacks teeth. The falcigers are coarsely serrated with less than

10 teeth on a blade.

Copulatory apparatus (Fig. 5Q; Plate IX: 6–8):

A male bears a single pair of copulatory apparatus on 19th or 20th setiger (Table 2). The ventral cirri of the segment are modified and elongated as thick, tapering processes, reaching nearly the end of the parapodial stem; they are situated in front of the copulatory organ proper and project ventrally; they are provided with long palpocils on their inner surface. The parapodial stems, the setae and the dorsal cirri remain unmodified there. The copulatory organ arises from the thick base of the parapodial stem ventro-laterally and elongates; it once rotates anteriorly to form a spiral structure subterminally; the distal end is developed as cuticular penis. From the spiral part arise two appendages; one is a minute spinous pad and the other is a small bidigitate process; they are situated face to face, the former anteriorly and the latter posteriorly, putting the penis between them. Apart from them, more basally, arises a larger bidigitate process.

Posterior end (Fig. 5R):

The pygidium expands laterally, ending in a round margin, though it carries no special organs or glands. It bears a pair of short anal cirri.

Remarks

The present material well agrees with *P. brevicirra* De Wilde & Govaere, 1995, in the size, the reduced condition of cephalic appendages, the shape of parapodia, and the arrangement of setae. The basic structure of the male copulatory apparatus such as the spirally wound copulatory organ with a basal bidigitate process, the elongated ventral cirrus, and the unmodified parapodial stem and setae, also coincides with that of *P. brevicirra*. However, the subterminal spinous pad found in the present material is absent in the latter. The flattened, semi-circular pygidium is also peculiar to the present material. Based on these differences, the present form is here erected as a new subspecies. The new name *platycauda* comes from the shape of the pygidium.

Pisone gopalai vannifera subsp. nov.

Pisone gopalai: Hartmann-Schröder & Parker, 1990: 195–200

Material. Seven males were collected from the lower intertidal zone of a sheltered beach

Table 3. Body size and position of copulatory apparatus in males of *Pisone gopalai vannifera* subsp. nov.

Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
6.8	49	19th	1379	holotype
4.6	37	17th	1380	paratype
7.3	51	16th	1381	paratype
4.0	28	14th	1382	paratype
6.3	49	18th	1383	SEM
4.2	35	16th	—	not preserved
6.2	44	19th	—	not preserved

of very coarse sand of Oura, Honjima Island, Marugame, Kagawa Prefecture (34°23'18"N, 133°46'07"E), in the Inland Sea of Japan, on May 16th, 1995. Type series is designated as shown in Table 3.

Diagnosis: Body length up to 7.3 mm. Prostomium distinct. Buccal segment characteristic of the genus; its posterior half widened. Ventral cirri of 1st setiger shorter than the parapodial stem. Dorsal cirri of 2nd setiger small, flask-shaped. Presetal lobes bilobed anteriorly and single in median and posterior segments. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal plate and three falcigers on a parapodium. A single pair of male copulatory apparatus of bulging appearance on an anterior or a middle segment; setae and ventral cirrus of the segment reduced; a hood ornamented with about 15 terminal, longitudinal ridges present; penis surrounded by the hood as a retractile, cuticular process; a fan-like appendage with stiff cuticular hairs projecting anteriorly; a large mass of spinous papillae developing posteriorly. Pygidium with caudal glands.

Holotype:

Male. Body length 6.8 mm with 49 setigers. Width of the trunk, exclusive of parapodia, 0.23–0.25 mm in anterior and middle portion of the body; its parapodial stems 0.18–0.21 mm long there; those of 1st setiger 0.09 mm long where the trunk being 0.19 mm wide. Brain extending back to the position of 3rd setiger. A pair of eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.15 mm long; buccal acicula 0.13 mm long; palpi 0.45 mm long; pharynx extending over 5–7th setigers. Ventral cirri of 1st setiger 0.04 mm long. Copulatory apparatus on 19th setiger. Anal cirri detached off.

Habitus (Plate I: 5):

The largest specimen attains a body length of 7.3 mm with 51 setigers (Table 3). The shape of the entire worm is slender, gradually tapering posteriorly. A single pair of male copulatory apparatus is situated on an anterior or a middle segment; it is conspicuous by its bulging appearance. Caudal organs are visible under transmitted light.

Colour:

White in alcohol.

Anterior end (Fig. 6A, B; Plate II: 7):

The prostomium is pentagonal in shape; it is situated far backwards compared with that of other species; its anterior median groove is as long as 0.05–0.07 mm. The brain extends back to the position of about 3rd setiger. A pair of eyes is located on the position of about 2nd setiger. The posterior half of the buccal segment is enlarged and widened; the dorsal cirri are elongated and cirriform; the ventral cirri are small, flask-shaped. The buccal acicula are well developed projecting through the skin anteriorly; their distal ends are much expanded with rounded margin (Fig. 4C). The palpi are thick and long. The pharynx extends over around 5–7th setigers. The jaws are devoid of inward projection (Fig. 6D).

Parapodia (Fig. 6E, F; Plate IV: 4, 5):

The ventral cirri of 1st setiger are about twice as long as those of the following segments. The dorsal cirri of 2nd setiger are the same in shape and size as those of the following segments. The presetal lobes are bilobed in anterior segments where the superior lobule is rather stump-shaped with terminal pores while the inferior one is pointed and

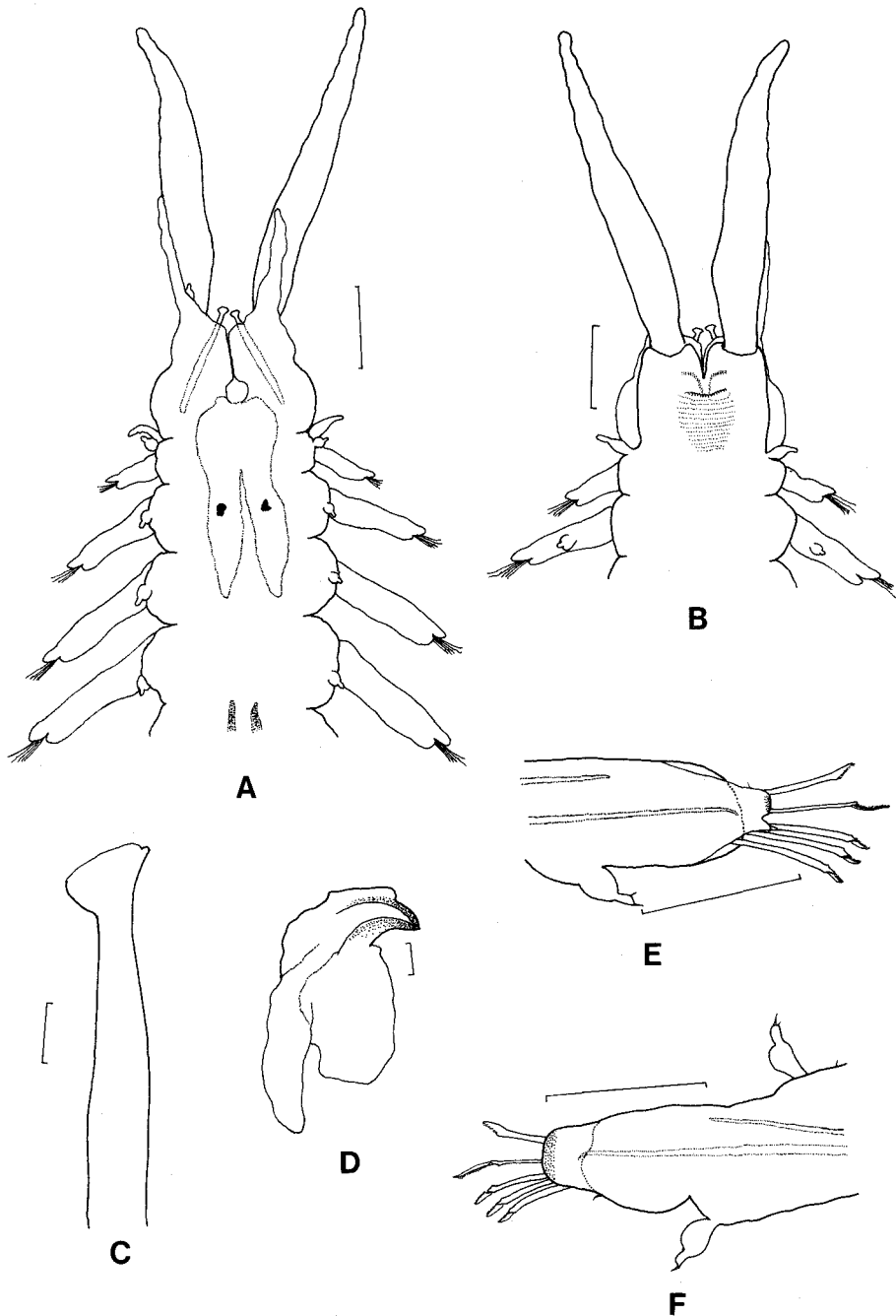


Fig. 6. *Pisione gopalai vannifera* subsp. nov. Holotype, Iv 1379. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (6th setiger); F. Anterior view of a median parapodium (27th setiger). Scale. A, B, E, F: 0.1 mm; C, D: 0.01 mm.

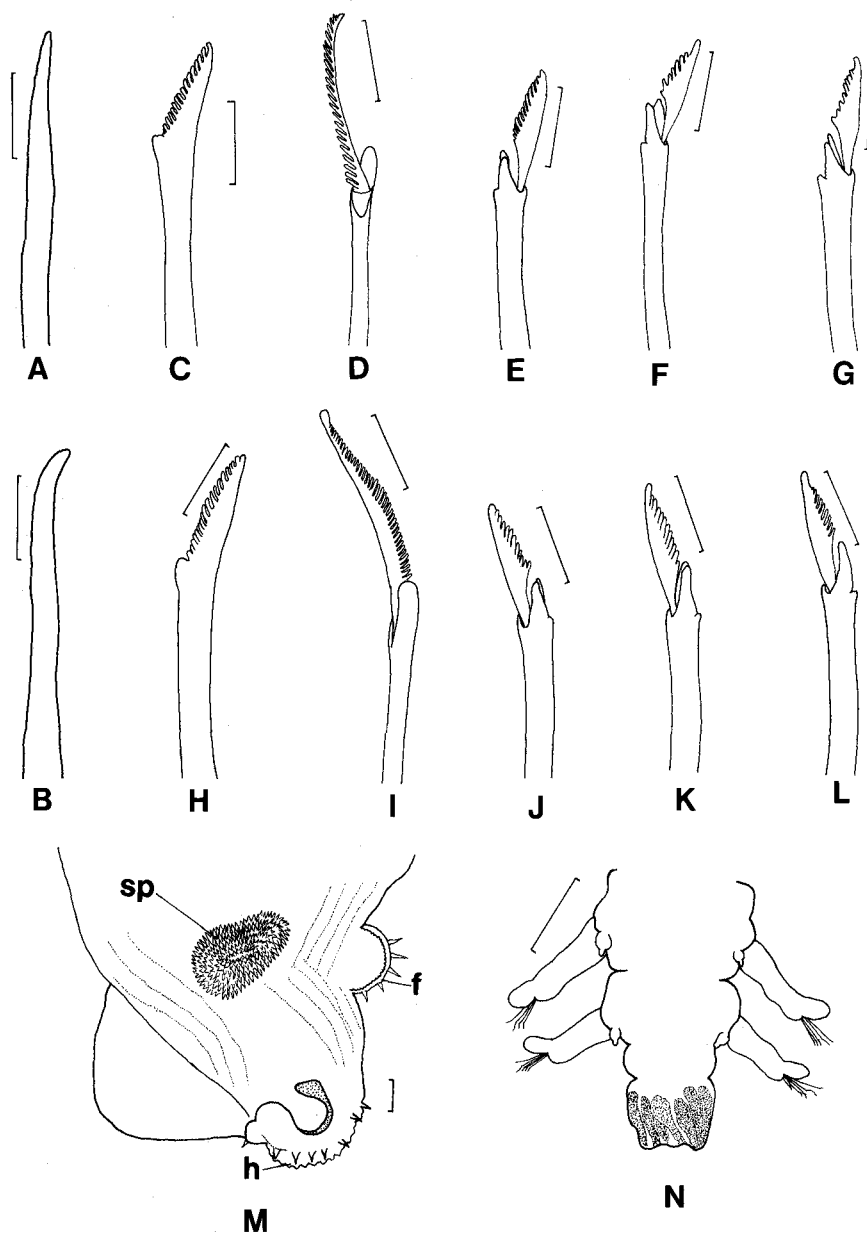


Fig. 7. *Pisone gopalai vannifera* subsp. nov. Holotype, Iv 1379. Male. A. Notoaciculum (25th setiger); B. Neuroaciculum (25th setiger); C. Supra-acicular simple seta (6th setiger); D. Long-bladed compound seta (6th setiger); E-G. Falcigers (6th setiger) from upper to lower; H. Supra-acicular simple seta (27th setiger); I. Long-bladed compound seta (27th setiger); J-L. Falcigers (27th setiger) from upper to lower; M. Posterior view of a copulatory organ (19th setiger); N. Dorsal view of posterior end (anal cirri detached). f: fan-like appendage; h: hood; sp: spinous papillae. Scale. A-L: 0.01 mm; M, N: 0.1 mm.

smaller without terminal pores. They become single in median and posterior segments; the lobe is spherical with many terminal pores.

The notoacacula are straight (Fig. 7A), while the neuroacacula curve ventrally at the tip (Fig. 7B).

Setae (Fig. 7C-L; Plate VI: 15-19):

There are one supra-acicular simple seta, one long-bladed compound seta and three falcigers on a parapodium. The distal part of the simple seta is obliquely truncate and serrated with 15-20 teeth along the edge. The blade of long-bladed compound seta is finely serrated with 20-30 teeth; the anterior side of the distal end of the shaft expands forming the anterior distal plate over the base of the blade. The upper and the middle falcigers are provided with 10-15 teeth on a blade while the lower with less than 10 teeth.

Copulatory apparatus (Fig. 7M; Plate X: 1, 2):

A single pair of male copulatory apparatus is situated in the anterior or middle region of the body, between 14-19th setiger (Table 3). The organ is the bulging structure formed by the fusion of the parapodial stem and the copulatory organ proper; it is supported by a long, embedded aciculum; setae are entirely reduced; the dorsal cirri remain unmodified while the ventral cirri are not recognized. The copulatory organ projects ventrally, with its end forming a hood ornamented with about 15 terminal, longitudinal ridges; each ridge is provided with a stiff spine; the penis is presumed to be surrounded by the hood as a retractile process. A fan-like appendage projects anteriorly from inside of the copulatory organ; it is provided with stiff cuticular hairs; they are also scattered on the inner surface of the hood. A remarkably large, circularly rimmed mass of spinous papillae develop posteriorly on the inner surface of the copulatory organ.

Posterior end (Fig. 7N; Plate V: 7-8):

The pygidium expands laterally and is transversely truncate at the end; it bears a pair of laterally separated caudal glands which are provided with several openings for secretion at the postero-lateral corners. A pair of slender anal cirri is present.

Remarks

The caudal gland, characteristic of the present material, is shared only with *P. gopalai* (Alikunhi, 1941). The fusion of parapodial stem to the copulatory organ proper and the loss of the setae and the ventral cirri on the male copulatory apparatus are also common to them. The present material, however, differs from *P. gopalai* in some detailed characters: the border of prostomium is distinct in the former whereas it is obscure in the latter; the copulatory apparatus bears a fan-like appendage in the former whereas it is absent in the latter. These differences seem to be rather slight and not fully significant enough to erect a new species, but should not be disregarded. The present material is, therefore, treated as a new subspecies of *P. gopalai*, whose new name *vannifera* is derived from "bearing a vannus(=fan)" on the male copulatory apparatus. In *P. gopalai* from Australia (Hartmann-Schröder & Parker, 1990) the prostomium is distinct in the text-figure (Fig. 1) and the fan-like appendage is considered to be described as "a second process with cuticular projections". Therefore, this form is regarded as identical with the present form. It should be pointed out that a slight difference exists between the two populations of the new subspecies: the tip of the neuroaciculum is expanded in the material of Australia (*loc. cit.*) whereas it is recurved ventrally in that of Japan.

***Pisione papuensis brevis* subsp. nov.**

Material. Fourteen males were collected from just below the lower extremity of intertidal zone of a semi-sheltered, very coarse sand beach of Busena, Nago City, Okinawa Island (26°32'07"N, 127°56'13"E), subtropical archipelago of southwestern Japan, on March 25th, 1992. Type series are designated as shown in Table 4.

Diagnosis: Body length up to 20.3 mm. Prostomium distinct. Buccal segment characteristic of the genus. Ventral cirri of 1st setiger even longer than dorsal cirri of buccal segment. Dorsal cirri of 2nd setiger small and flask-shaped. Presetal lobes single and spherical throughout the body. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal plate and three falcigers on a parapodium. Usually a single pair of male copulatory apparatus on a median or a posterior segment, with an additional pair sometimes appearing more posteriorly apart from the former; parapodial stem of the segment fused to the copulatory organ at the base leaving the presetal lobe and the two superior setae; ventral cirrus there bifurcated making a narrow space between them; copulatory organ proper coiling up anteriorly making a spiral behind the ventral cirrus. A long penis covered with short spines eversible from a spherical structure.

Holotype:

Male. Body length 15.6 mm with 101 setigers. Trunk usually exceeding 0.3 mm in width exclusive of parapodia; parapodial stems of 1st setiger about 0.1 mm long; they attaining 0.2 mm long at 4th setiger. Brain extending back to the position of 4th setiger. Paired eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.17 mm long; buccal acicula 0.18 mm long, entirely embedded; palpi 0.45 mm long; pharynx extending over 4–7th setigers. Ventral cirri of 1st setiger 0.21 mm long. Copulatory apparatus on 50th setiger. Anal cirri 0.6 mm long.

Habitus (Plate I: 6):

Body length attains 20.3 mm; the maximal number of setigers are 104 (Table 4). The entire worm is long and thick gradually tapering posteriorly. The paired male copulatory apparatus are conspicuous with bulging appearance on one of the median segments; sometimes an additional pair may be present separately.

Colour:

White in alcohol.

Anterior end (Fig. 8A, B; Plate II: 8):

The prostomium is diamond-shaped. The brain extends back to the position of about 4th setiger. One pair of eyes is located at the position of about 2nd setiger. Buccal segment tapers anteriorly; its dorsal cirri are slender and cirriform; ventral cirri are small, flask-shaped. Buccal acicula are well-developed (Fig. 8C) sometimes entirely embedded in the segment not projecting through the skin. Palpi are thick and long. The pharynx extends over around 4–7th setigers. The jaws are devoid of inward projection (Fig. 8D).

Parapodia (Fig. 8E, F; Plate IV: 6):

The ventral cirri of 1st setiger are so much elongated as to exceed the length of the dorsal cirri of the buccal segment. The dorsal cirri of 2nd setiger are small, flask-shaped. The presetal lobes are uniformly single and spherical with many terminal pores.

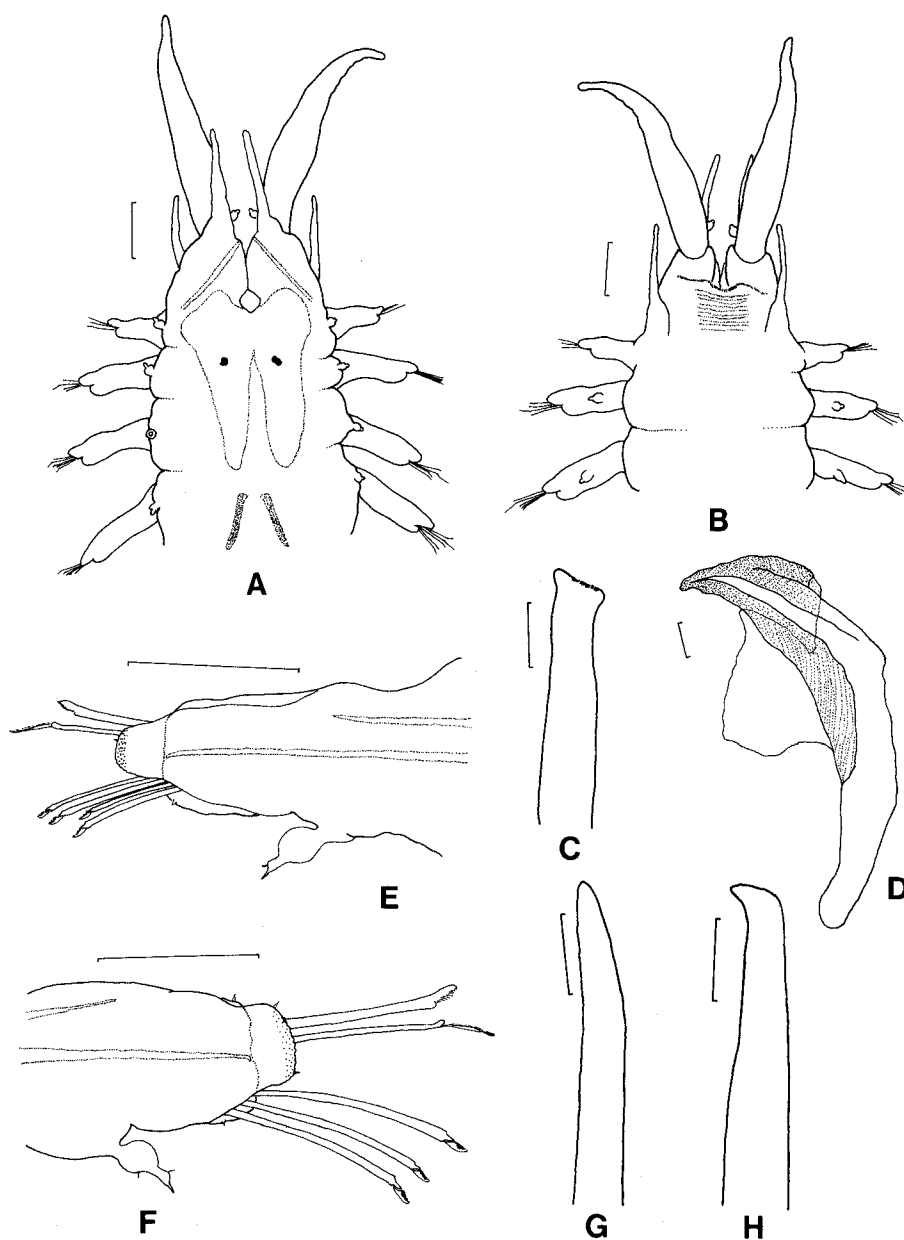


Fig. 8. *Pisione papuensis brevis* subsp. nov. Holotype, Iv 1384. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (5th setiger); F. Anterior view of a median parapodium (53rd setiger); G. Notoaciculum (59th setiger); H. Neuroaciculum (59th setiger). Scale. A, B, E, F: 0.1 mm; C, D, G, H: 0.01 mm.

The notoaicula are straight (Fig. 8G), while the neuroacacula curve ventrally at the tip (Fig. 8H).

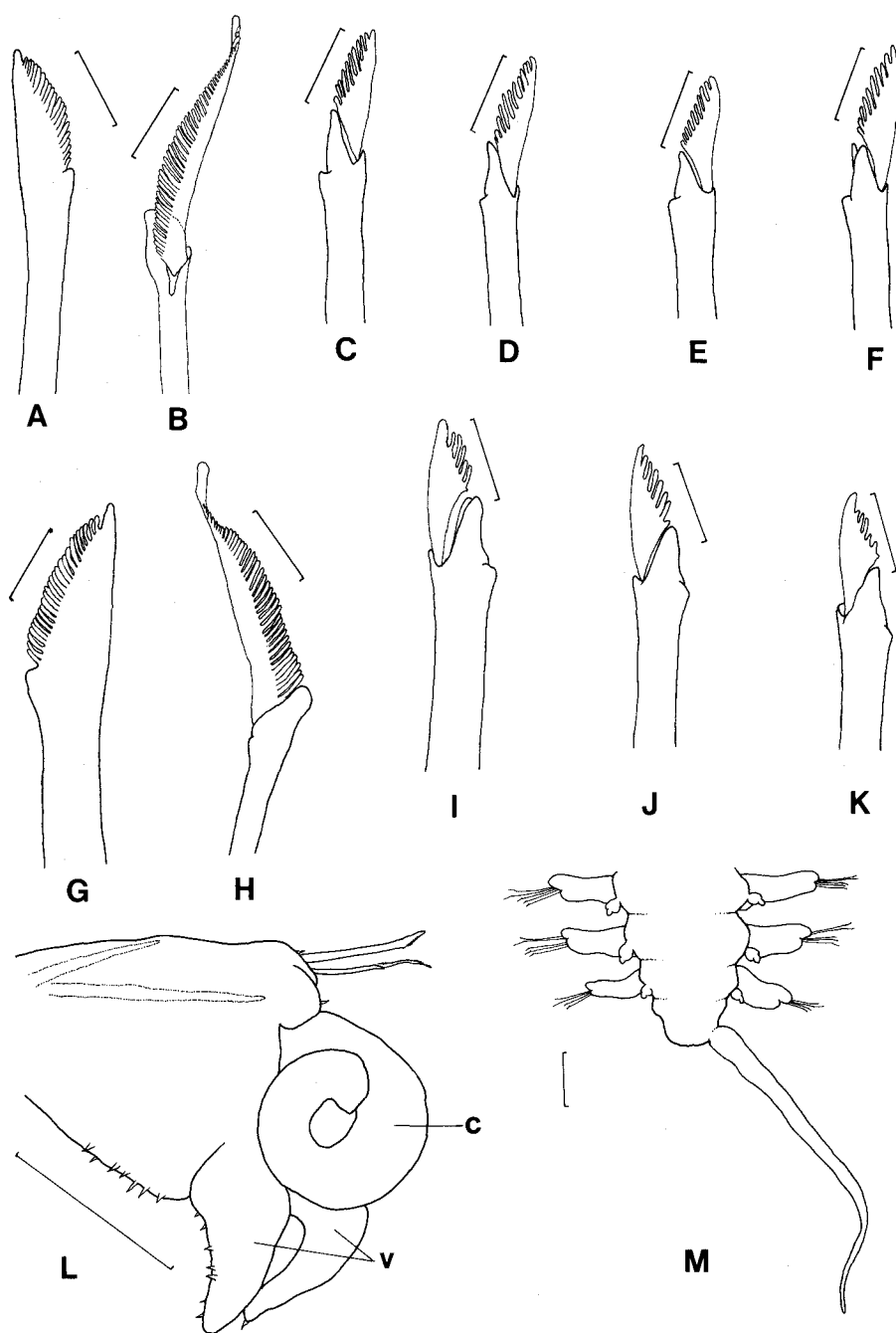


Fig. 9. *Pisone papuensis brevis* subsp. nov. Holotype, Iv 1384. Male. A. Supra-acicular simple seta (4th setiger); B. Long-bladed compound seta (4th setiger); C-F. Falcigers (4th setiger) from upper to lower; G. Supra-acicular simple seta (59th setiger); H. Long-bladed compound seta (59th setiger); I-K. Falcigers (59th setiger) from upper to lower; L. Anterior view of a copulatory organ (50th setiger); M. Dorsal view of posterior end. c: copulatory organ proper; v: ventral cirrus. Scale. A-K: 0.01mm; L, M: 0.1mm.

Setae (Fig. 9A-K; Plate VII: 1-5):

There are one supra-acicular simple seta, one long-bladed compound seta and three or rarely four falcigers on a parapodium. The distal end of the simple seta is obliquely truncate and serrated with 20-25 teeth along the edge; an outline drawn by connecting the ends of the teeth shows an arc-like appearance. The blades of long-bladed compound setae are finely serrated with 30-50 teeth; the anterior side of the distal end of the shaft stretches obliquely towards the cutting edge of the blade forming the anterior distal plate which covers the basal part of the blade. These two setae are always situated only a short distance apart, giving an appearance that both project from supra-acicular position; close examination, however, has revealed that the former projects from the supra-acicular position while the latter projects from the infra-acicular position, which is the case in other species. The falcigers are rather coarsely serrated with 5-8 teeth on a blade.

Copulatory apparatus (Fig. 9L; Plate X: 3-4):

A mature male usually carries a single pair of copulatory apparatus on a median or a posterior segment, mostly around 50th setiger; an additional pair sometimes appears more posteriorly apart from the former (Table 4). These fertile segments are twice as long as other segments. The anterior half of the segment contains sperm sacs. The testes prevail into two or three foregoing segments. The parapodial stem is expanded widely, rectangular in ventral view with the presetal lobe conspicuous at the postero-lateral corner; it bears the supra-acicular simple seta and the long-bladed compound seta while the falcigers are absent. The ventral cirrus projects inward from the inner margin of the parapodial stem and bends anteriorly; it is so much modified as to be bifurcated from the basal part making a narrow space between them. The copulatory organ arises from beneath the parapodial stem posteriorly and coils up anteriorly making a spiral behind the ventral cirrus; its terminal portion enters into the space between the branches of the bifurcate ventral cirrus and is usually concealed. According to the SEM observation (Plate X: 4), a storage of the penis of a spherical appearance is formed in the inner part of the spiral, from which the long

Table 4. Body size and position of copulatory apparatus in males of *Pisione papuensis brevis* subsp. nov.

Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
15.6	101	50th	1384	holotype
14.5	100	48th & 71st	1385	paratype
12.0	93	58th	1386	paratype
13.9	90	45th	1387	paratype
12.6	> 70	49th & 65th	1388	paratype
16.2	104	46th	1389	paratype
13.0	98	44th	1390	paratype
13.9	84	77th	1391	paratype
14.8	98	41st & 66th	1392	paratype
16.3	104	49th	1393	paratype
20.3	97	60th	1394	paratype, SEM
8.3	> 65	50th	1395	paratype, SEM
—	—	—	1396	paratype, SEM
—	—	—	1397	paratype, SEM

penis covered with short spines is protrusile into the space between the branches of the ventral cirrus.

Posterior end (Fig. 9M):

The pygidium tapers posteriorly bearing a pair of slender anal cirri.

Remarks

The present material well agrees with *P. papuensis* Govaere & De Wilde, 1993, from Papua New Guinea, in the specific characters including the details of male copulatory apparatus. A slight, but distinct difference, however, exists between them in the dorsal cirrus of 2nd setiger: it is small, flask-shaped in the former whereas it is "more than twice as long as on other segments" in the latter. It seems, therefore, to be appropriate to distinguish them in subspecies level; the difference is presumably due to the geographic distance between the two populations. Recently, De Wilde & Govaere (1995) revealed the presence of spinous papillae on the male copulatory apparatus. The organ has not been observed in the present material. The name of the new subspecies *brevis* comes from the "short" dorsal cirri of 2nd setiger.

The long, retractile penis covered with spines and its spherical storage are newly revealed in the present study.

Pisone bulbifera sp. nov.

Material. Six male, and one sexually undetermined specimens were collected from the subtidal sandy bottom of 5 m deep near the mouth of Amitori Bay, northwestern part of Iriomote Island, Taketomi-cho, Yaeyama Islands (24°17'46"N, 123°40'11"E), subtropical archipelago of southwestern Japan, on April 23rd 1995. Type series are designated as shown in Table 5.

Diagnosis: Body length up to 7.2 mm. Prostomium spindle-shaped. Buccal segment characteristic of the genus. Ventral cirri of 1st setiger, with a bulbous swelling subterminally, nearly as long as the parapodial stem of the same segment. Dorsal cirri of 2nd setiger small, flask-shaped. Presetal lobes bilobed anteriorly and single posteriorly. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal plate and three falcigers on a parapodium. A single pair of male copulatory apparatus on an anterior segment; the parapodial stems and setae of the segment unmodified, while the ventral cirri elongated. Copulatory organ proper elongated, gradually curving inward;

Table 5. Body size and position of male copulatory apparatus in *Pisone bulbifera* sp. nov.

Sex	Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
male	7.1	56	21st	1399	holotype
male	2.8	25	19th	1400	paratype
male	6.3	51	26th	1401	paratype
male	7.2	43	21st	1402	paratype
male	6.7	60	24th	1403	paratype
?	4.8	36	absent	1404	paratype
male	6.0	47	21st	1405	paratype, SEM

it turns up making a knob and a spinous pad subterminally, and ends in a digitated process without forming a spiral; another knob present more basally.

Holotype:

Male. Body length 7.1 mm with 56 setigers. Width of the trunk, exclusive of parapodia, around 0.20 mm throughout. Parapodial stem around 0.15 mm long except for that of 1st setiger with 0.08 mm long. Brain extending back to the position between 3rd and 4th setiger. Paired eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.12 mm long; buccal acicula 0.18 mm long, without remarkable expansions distally; palpi 0.40 mm long; pharynx extending over 4–7th setigers. Ventral cirri of 1st setiger 0.12 mm long. Copulatory apparatus on 21st setiger.

Habitus (Plate I: 7):

Body length attains 7.2 mm; the maximal number of setigers is 60 (Table 5). The entire worm is short and slender hardly tapering posteriorly. A single pair of male copulatory apparatus is conspicuous bulging laterally at one of the anterior segments. Parapodial stems are a little shorter than the width of the same segment except for some anterior ones where they are much shorter; those of 1st setiger are about half the width of the segment.

Colour:

White in alcohol.

Anterior end (Fig. 10A, B; Plate III: 1, 2):

The border of the prostomium is rather obscure except for its anterior margin; SEM observation has revealed its spindle-shaped outline vaguely. The brain extends back to the position of 3rd or 4th setiger. One pair of eyes is located at the position of about 2nd setiger. The lateral margins of the buccal segment are parallel to each other not tapering anteriorly. The dorsal cirri of the buccal segment are long and cirriform; the ventral cirri are small, flask-shaped. The buccal acicula are well developed projecting through the skin anteriorly; their distal ends are truncate, without remarkable expansions in the holotype (Fig. 10C). The palpi are thick and long. The pharynx extends over around 4–7th setigers. The jaws are devoid of inward projection (Fig. 10D).

Parapodia (Fig. 10E, F; Plate IV: 7, 8):

The ventral cirri of 1st setiger, with a bulbous swelling subterminally, are nearly as long as the parapodial stem of the same segment. The dorsal cirri of 2nd setiger are the same shape and size as those of the following segments. The presetal lobes are bilobed anteriorly; the superior lobule is digitiform with terminal pores while the inferior one is pointed and smaller without pores. They become single in median and posterior segments, expanding spherically with many terminal pores.

The notoacacula are straight (Fig. 11A); the neuroacacula are also nearly straight (Fig. 11B).

Setae (Fig. 11C-L; Plate VII: 6–10):

There are one supra-acicular simple seta, one long-bladed compound seta and three falcigers on a parapodium. The distal end of the simple setae is obliquely truncate and serrated with 15–20 teeth along the edge. The blade of long-bladed compound setae are finely serrated with about 30 teeth; the anterior side of the distal end of the shaft expands forming the anterior distal plate over the base of blade. The upper and the middle falcigers

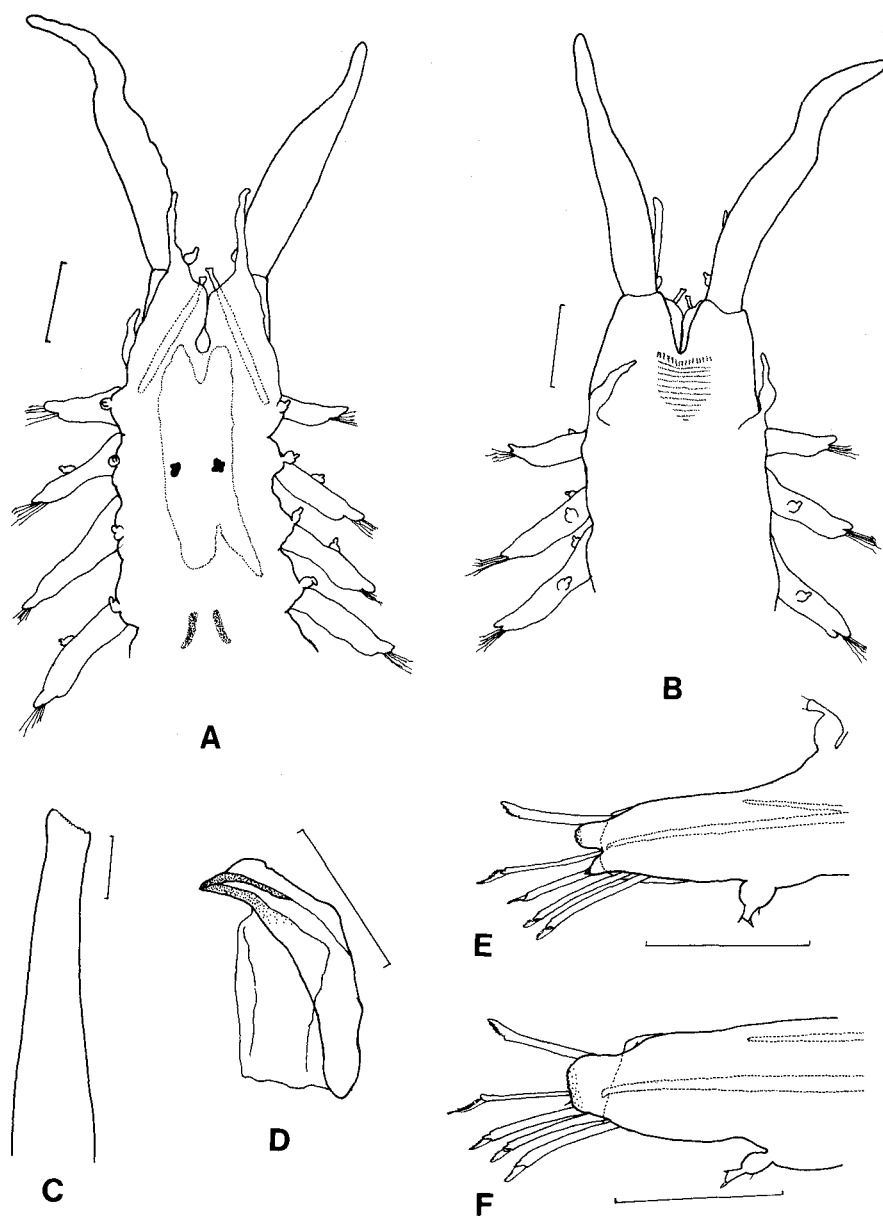


Fig. 10. *Pisione bulbifera* sp. nov. Holotype, Iv 1399. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (5th setiger); F. Anterior view of a median parapodium (30th setiger). Scale. A, B, E, F: 0.1 mm; C, D: 0.01 mm.

are provided with 10–15 teeth on a blade while the lower with less than 10 teeth.

Copulatory apparatus (Fig. 11M; Plate X: 5–6):

A male bears a single pair of copulatory apparatus in the range of 19–26th setiger (Table 5). The ventral cirri of these segments are modified and elongated as thick,

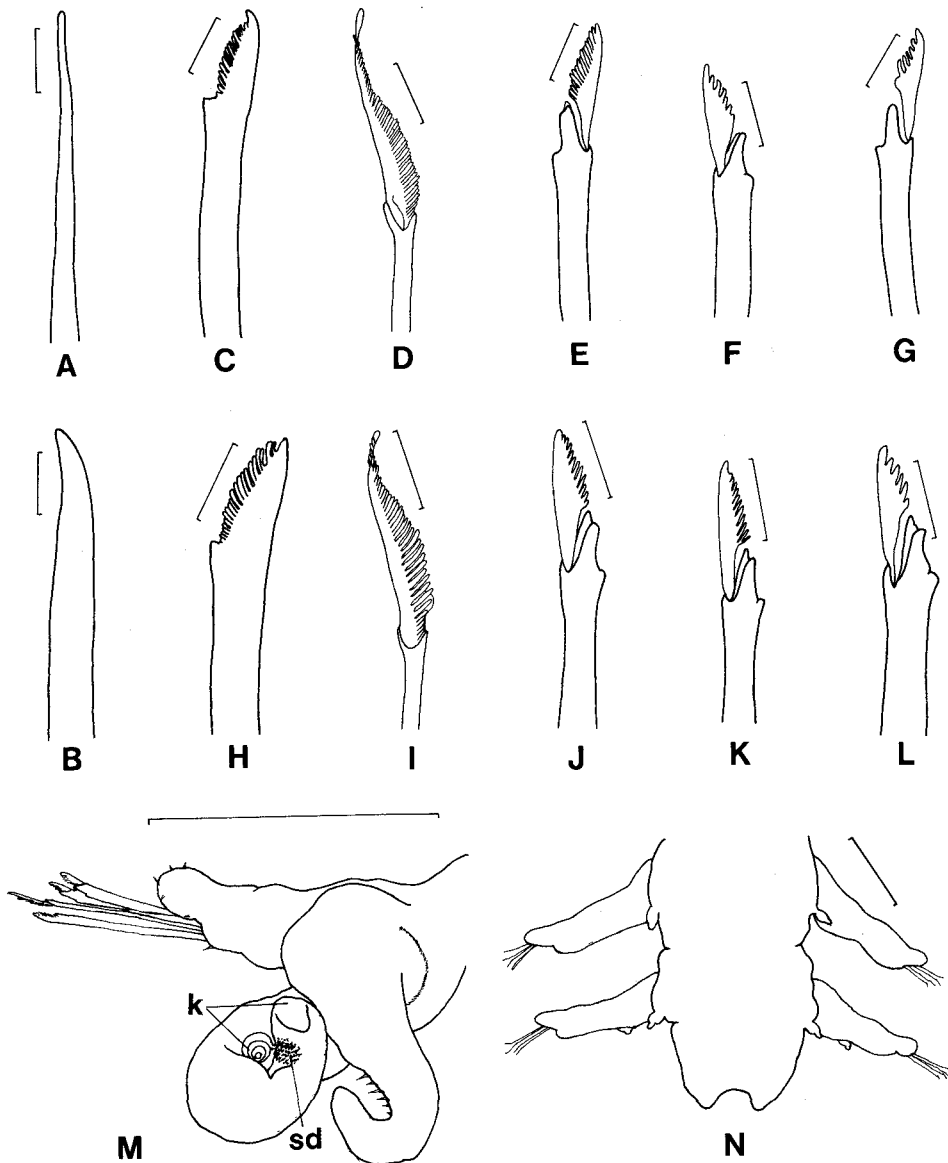


Fig. 11. *Pisione bulbifera* sp. nov. Holotype, Iv 1399. Male. A. Notoaciculum (30th setiger); B. Neuroaciculum (30th setiger); C. Supra-acicular simple seta (5th setiger); D. Long-bladed compound seta (5th setiger); E. Superior falciger (4th setiger); F. Median falciger (5th setiger); G. Lower falciger (4th setiger); H. Supra-acicular simple seta (30th setiger); I. Long-bladed compound seta (30th setiger); J-L. Falcigers (30th setiger) from upper to lower; M. Lateral view of a copulatory organ (21st setiger); N. Dorsal view of posterior end (anal cirri detached). k: knobs; sd: spinous pad. Scale. A-L: 0.01 mm; M, N: 0.1 mm.

tapering processes nearly as long as the parapodial stem; they are situated in front of the copulatory organ and project ventrally provided with many palpocils. The parapodial stems, the setae and the dorsal cirri remain unmodified there. The copulatory organ proper arises from the thick base of the parapodial stem ventro-laterally and elongates; it gradually curves inward and turn up ending in a digitated process; it is provided with a subterminal

knob, close to which develops a spinous pad. Apart from these appendages, more basally, develops another knob on the inner side of the copulatory organ.

Posterior end (Fig. 11N):

The pygidium tapers posteriorly. The anal cirri are considered to be detached and lost in the material examined.

Remarks

The combination of characters such as the elongated ventral cirri of 1st setiger, the small dorsal cirri of 2nd setiger, the presence of the long-bladed compound setae and the absence of the infra-acicular simple setae in the present material is common to *P. alikunhii* Tenerelli, 1965, *P. galapagoensis* Westheide, 1974, *P. laubieri* Hartmann-Schröder, 1970, *P. martinsi* Hartmann-Schröder, 1974, *P. helenae* De Wilde & Govaere, 1995, *P. primitiva* De Wilde & Govaere, 1995, *P. parhelenae* De Wilde & Govaere, 1995 *P. papuensis brevis* subsp. nov. and *P. umbraculifera* sp. nov. in the genus. They can be distinguished from each other by comparing their male copulatory apparatus. The parapodial stems of male fertile segments are more or less modified or reduced in most of these species; both the parapodial stems and the setae remain unmodified only in *P. helenae*, *P. umbraculifera*, *P. primitiva* and the present form. The former two species, however, bear cuticular plate, which is absent in the present material, on the copulatory organ proper. *P. primitiva* and the present material can be distinguished by the notoacacula of parapodia projecting through body wall in the former. The bulbous expansion of the ventral cirrus of 1st setiger is also peculiar to the present material. Therefore, the form in question is erected here as a new species whose name is derived from the shape of the ventral cirri of 1st setiger.

Pisione mista sp. nov.

Material. One sexually undetermined specimen was obtained from the lower intertidal slope of Sakai-ura, a semi-exposed, very coarse sand beach of Chichi-jima, Bonin Islands, Ogasawara, Tokyo (27°04'50"N, 142°12'15"E), isolated subtropical islands of southern Japan, on January 9th, 1995. It is designated as the holotype with a registration number of Iv 1406.

Diagnosis: Thick species, trunk up to 1.4 mm wide exclusive of parapodia. Prostomium distinct. Buccal segment well developed with thick acicula not projecting through the skin. First setiger together with its parapodia less developed except for the long ventral cirri. Dorsal cirri of 2nd setiger more than twice as long as the parapodial stem. Presetal lobes bilobed throughout; in anterior segments, the superior lobule with a round, and the inferior with an acute tip; in median and posterior segments, the superior lobule broad and thick, and the inferior club-shaped. In posterior segments, enlarged notoacacula projecting through body wall. One obliquely truncate simple seta from supra-acicular position, two or more long-bladed compound setae with anterior distal plate, and three or four falcigers from infra-acicular position. An additional simple setae from infra-acicular position emerging on posterior segments. Pygidium short with thread-like anal cirri.

Habitus (Plate I: 8):

The single specimen is 24.9 mm long with 121 setigers. Width of the trunk exclusive of parapodia is 0.7 mm at buccal segment, 1.2 mm at 6th setiger and gradually increases up to 1.4 mm at around 60th setiger; it abruptly tapers at the last ten setigers. Lengths of parapodial stems are 0.11 mm at 1st, 0.19 mm at 2nd, 0.28 mm at 3rd setiger and gradually increases up to about 0.4 mm. First setiger is less developed and rather inconspicuous. In posterior segments, notoacacula enlarge and project through

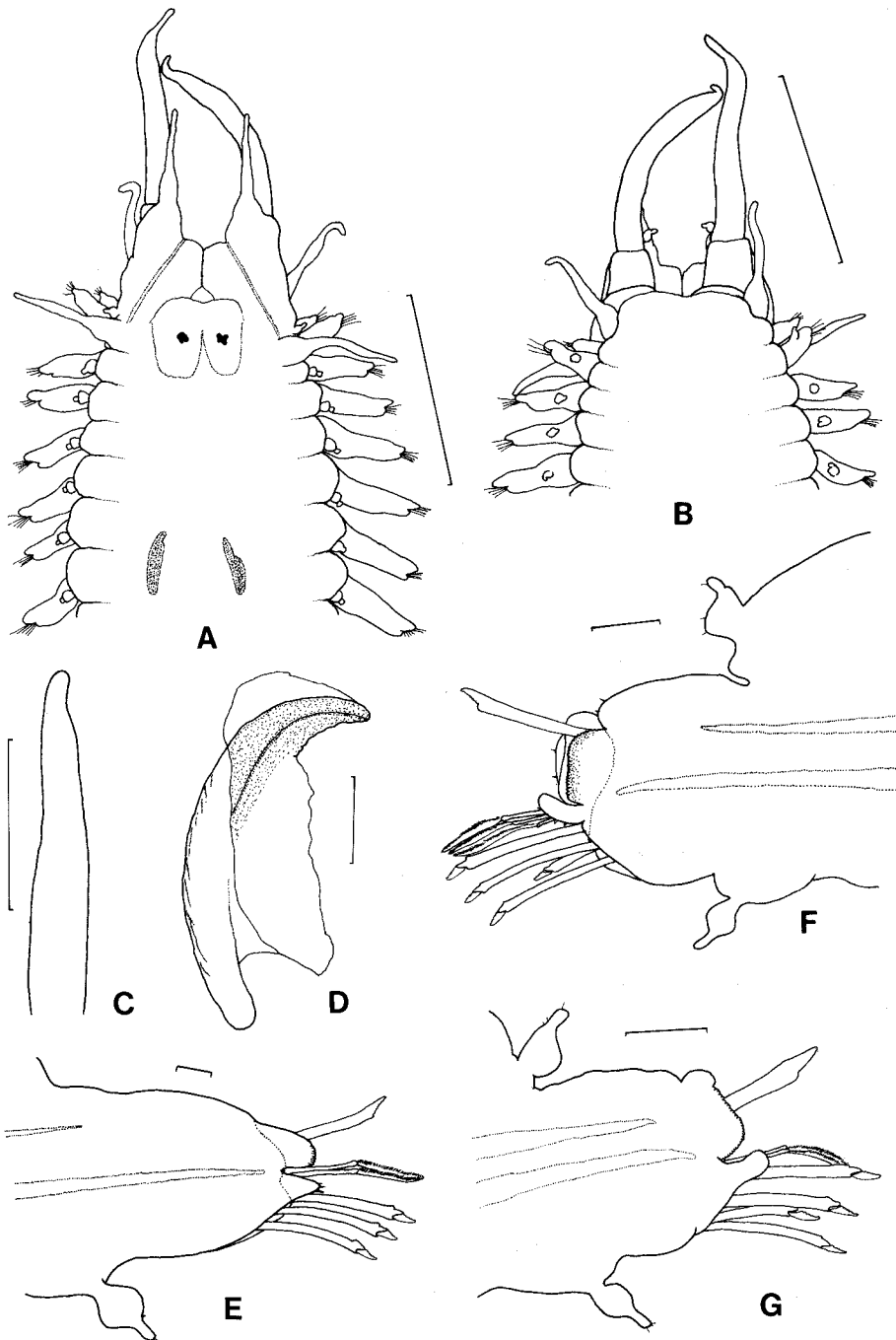


Fig. 12. *Pisione mista* sp. nov. Holotype, Iv 1406. A. dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (7th setiger); F. Anterior view of a median parapodium (57th setiger); G. Anterior view of a posterior parapodium (108th setiger). Scale. A, B: 1 mm; C-G: 0.1 mm.

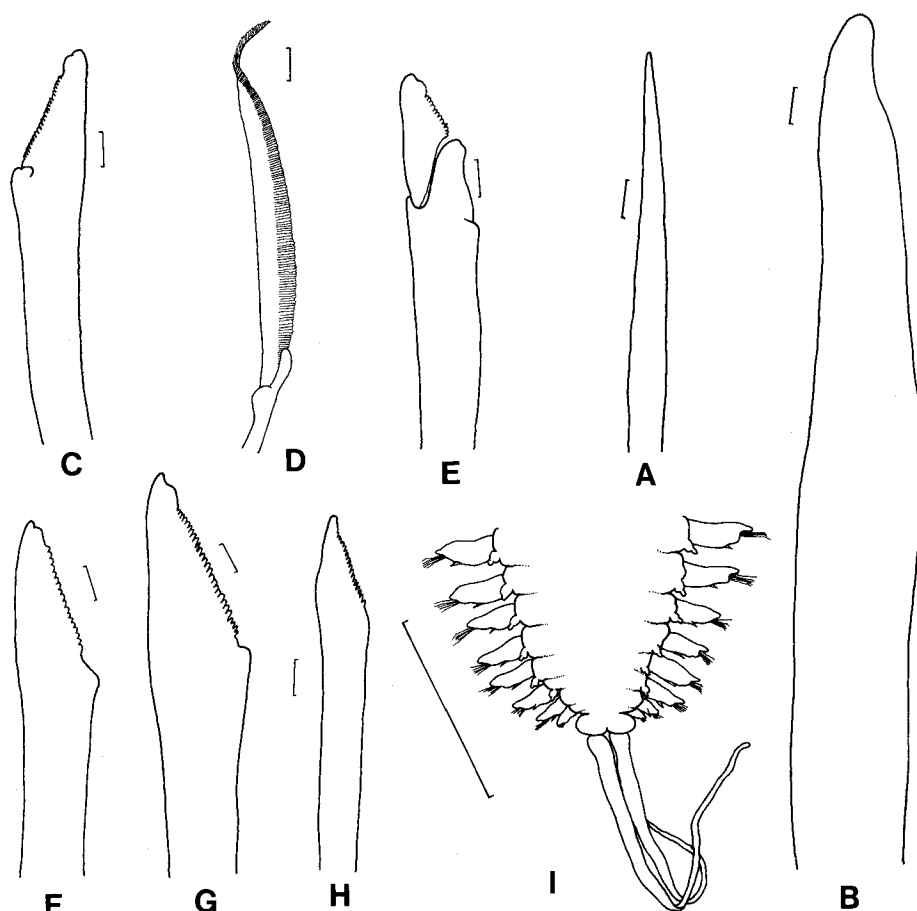


Fig. 13. *Pisione mista* sp. nov. Holotype, Iv 1406. A. Notoaciculum (7th setiger); B. Notoaciculum (109th setiger); C. Supra-acicular simple seta (57th setiger); D. Long-bladed compound seta (57th setiger); E. Falciger (57th setiger). F. Infra-acicular simple seta (108th setiger); G. Supra-acicular simple seta (109th setiger); H. Infra-acicular simple seta (109th setiger); I. Dorsal view of posterior end. Scale. A-H: 0.01 mm; I: 1 mm.

the body wall postero-dorsally.

Colour:

Yellowish brown in alcohol.

Anterior end (Fig. 12A, B):

The prostomium is visible as a small, triangular structure led by an anterior, median groove. The brain is posteriorly bilobed extending to the position of 3rd setiger. A pair of eyes of irregular shape is situated on the brain. The buccal segment is well-developed; the dorsal cirri project forwards with lengths of 0.6 mm; ventral cirri are small, flask-shaped; buccal acicula are amber-colored with lengths of 0.5 mm; their anterior ends are blunt without expansions (Fig. 12C); they do not project through body wall; they arise from the basal part of the parapodia of 2nd setiger. The palpi taper gradually, with lengths of 1.1 mm. The jaws are located at the position of 7-8th setiger; they lack inward projection and carry a hood-like extension posteriorly (Fig. 12D).

Parapodia (Fig. 12E-G; Plate V: 1)

The ventral cirri of 1st setiger are slightly longer than the dorsal cirri of buccal segment with lengths of 0.65 mm. The dorsal cirri of 2nd setiger, 0.55 mm long, are more than twice as long as the parapodial stem of the same segment. The presetal lobes are bilobed throughout the body; in anterior segments, both of the lobules are subequal in size, and the tip of the superior is rounded while that of the inferior is pointed; in median and posterior segments, the superior is broad and thick encircled by thin membrane and are provided with fine terminal pores, while the inferior is smaller and club-shaped. The postsetal lobes are less developed than the presetal lobes and shallowly bilobed; the superior is larger and circular while the inferior is smaller and bluntly triangular.

Both the notoacacula and the neuroacacula are straight. The former is thin in anterior segments (Fig. 13A) and enlarges in posterior segments nearly as thick as the neuroacaculum of the same parapodium (Fig. 13B) and from about 70th setiger on its distal end emerges out breaking the postero-dorsal wall of the parapodial stem.

Setae (Fig. 13C-H; Plate VII: 11-15):

There are one simple seta from supra-acicular position, two or more long-bladed compound setae and three or four falcigers from infra-acicular position on a parapodium. The distal part of the supra-acicular simple seta is obliquely truncate and weakly serrated with about 18 teeth along the edge. The blade of the long-bladed compound setae are slender and bear extremely fine serration with more than 100 teeth; the anterior side of the distal end of the shaft expands forming an oval, spatula-like plate (=anterior distal plate) and covers some part of the base of the blade. The serration of the falciger is weak with about 10 teeth on a blade. The distal ends of both the supra-acicular simple setae and the falcigers have knob-like, bluntly bifid appearances. On a posterior segment, 109th setiger, an infra-acicular simple seta was observed to coexist with the supra-acicular simple seta. More posteriorly, the supra-acicular simple setae are disappeared and replaced by the infra-acicular ones; these two different types of simple setae are very similar in shape.

Posterior end (Fig. 13I):

The pygidium is short, expanding laterally. A pair of anal cirri is long and slender with lengths of 1.7 mm.

Remarks

The present material is closely related to *P. oerstedii pulla* Westheide, 1974 from Galapagos, in the shape of presetal lobe with club-shaped inferior lobule and of long-bladed compound setae with markedly fine serration, both of which are exclusively represented by these two forms in the genus. In the latter, however, prostomium is indistinct and buccal acicula are absent. The nominotypical subspecies, *P. oerstedii oerstedii* Grube, 1857, from the west coast of South America, possesses buccal acicula, but it lacks the long-bladed compound setae, the presetal lobes are single, and the prostomium is indistinct. The present material is thus characteristic by the possession of all these characters, hence the name "mista" (=mixed). In addition, the infra-acicular simple setae of the present material has not been recognized in other two forms. Although the two subspecies of *P. oerstedii* and the present form are characterized by the extremely larger size and the marked elongation of dorsal cirri of 2nd setiger, they should be treated as distinct species because every difference shown above is significant enough to separate species in the genus.

Pisione paucisetosa sp. nov.

Material. Twelve male and three sexually undetermined specimens were collected from the lower intertidal slope of Miyano-hama, an exposed, very coarse sand beach of Chichi-jima, Bonin Islands, Ogasawara, Tokyo (27°06'03"N, 142°11'25"E), isolated subtropical islands of southern Japan, on January 9th, 1995. Type series are designated as shown in Table 6.

Table 6. Body size and position of male copulatory apparatus in *Pisione paucisetosa* sp. nov.

Sex	Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
male	8.9	60	47th	1407	holotype
male	7.2	64	54th	1408	paratype
male	6.7	56	44th	1409	paratype
male	5.5	49	40th	1410	paratype
male	7.9	53	40th	1411	paratype
male	6.4	69	50th	1412	paratype
male	5.3	52	43rd	1413	paratype
male	5.0	54	45th	1414	paratype
male	7.0	63	46th	1415	paratype
male	7.2	61	46th	1416	paratype
?	11.6	76	absent	1417	paratype
?	7.6	48	absent	1418	paratype
?	8.0	57	absent	1419	paratype
male	?	?	present	1420	paratype, SEM
male	?	?	present	1421	paratype, SEM

Diagnosis: Body length up to 11.6 mm. Ventral surface of posterior trunk spotted by dark pigments. Prostomium obscure. Buccal segment characteristic of the genus. Buccal aciculum well developed projecting through the skin. Ventral cirri of 1st setiger nearly as small as those of other segments. Dorsal cirri of 2nd setiger not elongated. Presetal lobes bilobed anteriorly and single posteriorly. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal plate and two falcigers on a parapodium. Single pair of male copulatory apparatus on a posterior segment; setae and ventral cirri absent; a hood ornamented with about 10 longitudinal ridges present; penis surrounded by the hood as a retractile process; a fan-like appendage with stiff cuticular hairs projecting anteriorly; three conspicuous masses of spinous papillae present.

Holotype:

Male. Body length 8.9 mm with 60 setigers. Trunk usually about 0.3 mm wide exclusive of parapodia; the parapodial stem of 1st setiger only about 0.07–0.08 mm long; in the anterior ten segments they attaining lengths of 0.17–0.2 mm. Brain extending back to the position of 3rd setiger. Paired eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.15 mm long; buccal acicula 0.10 mm long; palpi 0.35 mm long; pharynx extending over 4–7th setigers. Ventral cirri of 1st setiger 0.04 mm long. Copulatory apparatus on 47th setiger. Anal cirri 1.0 mm long.

Habitus (Plate I: 9):

The largest specimen attains a body length of 11.6 mm with 76 setigers (Table 6). The

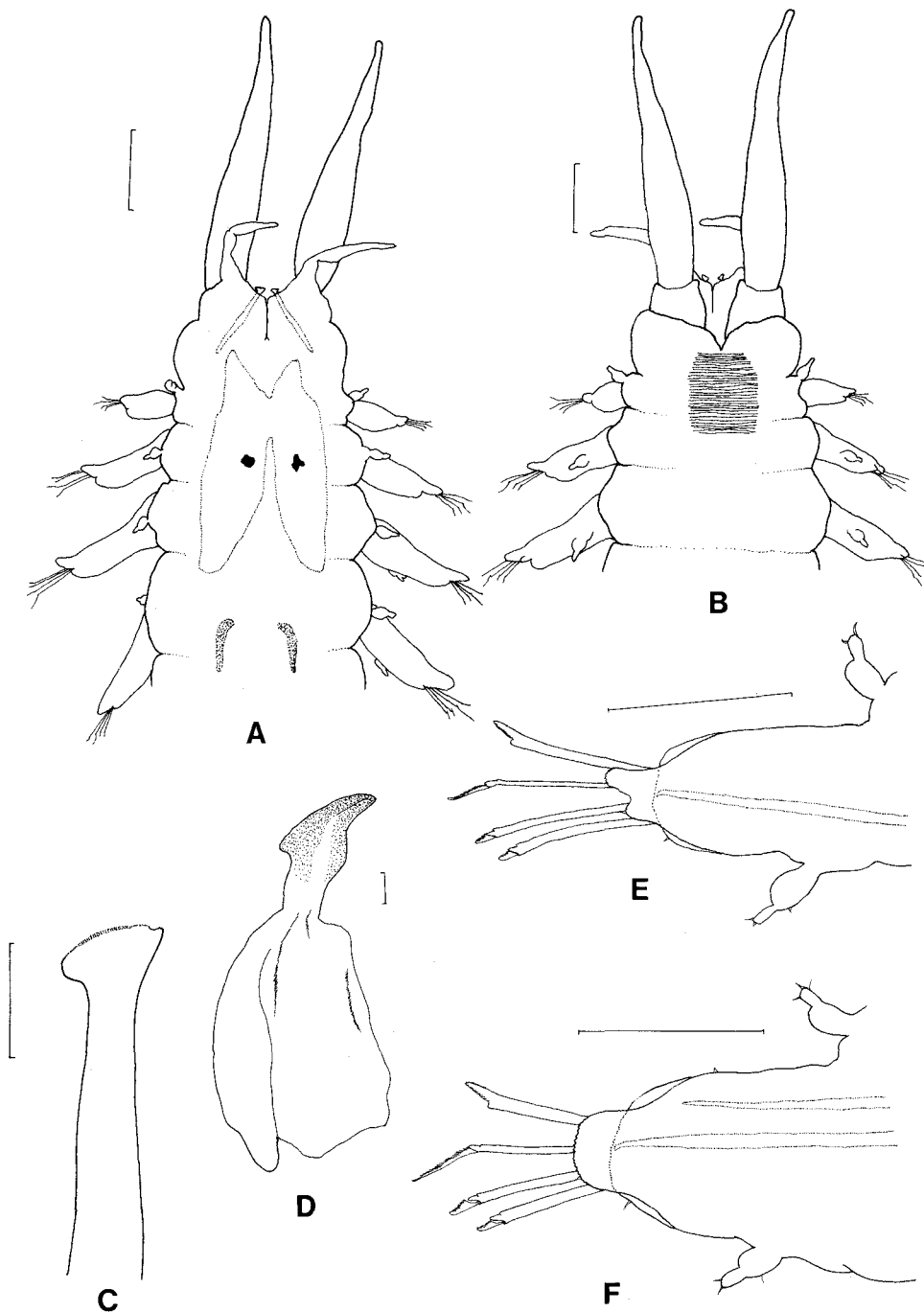


Fig. 14. *Pisione paucisetosa* sp. nov. Holotype, Iv 1407. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (4th setiger); F. Anterior view of a median parapodium (33rd setiger). Scale: A, B, E, F: 0.1 mm; C, D: 0.01 mm.

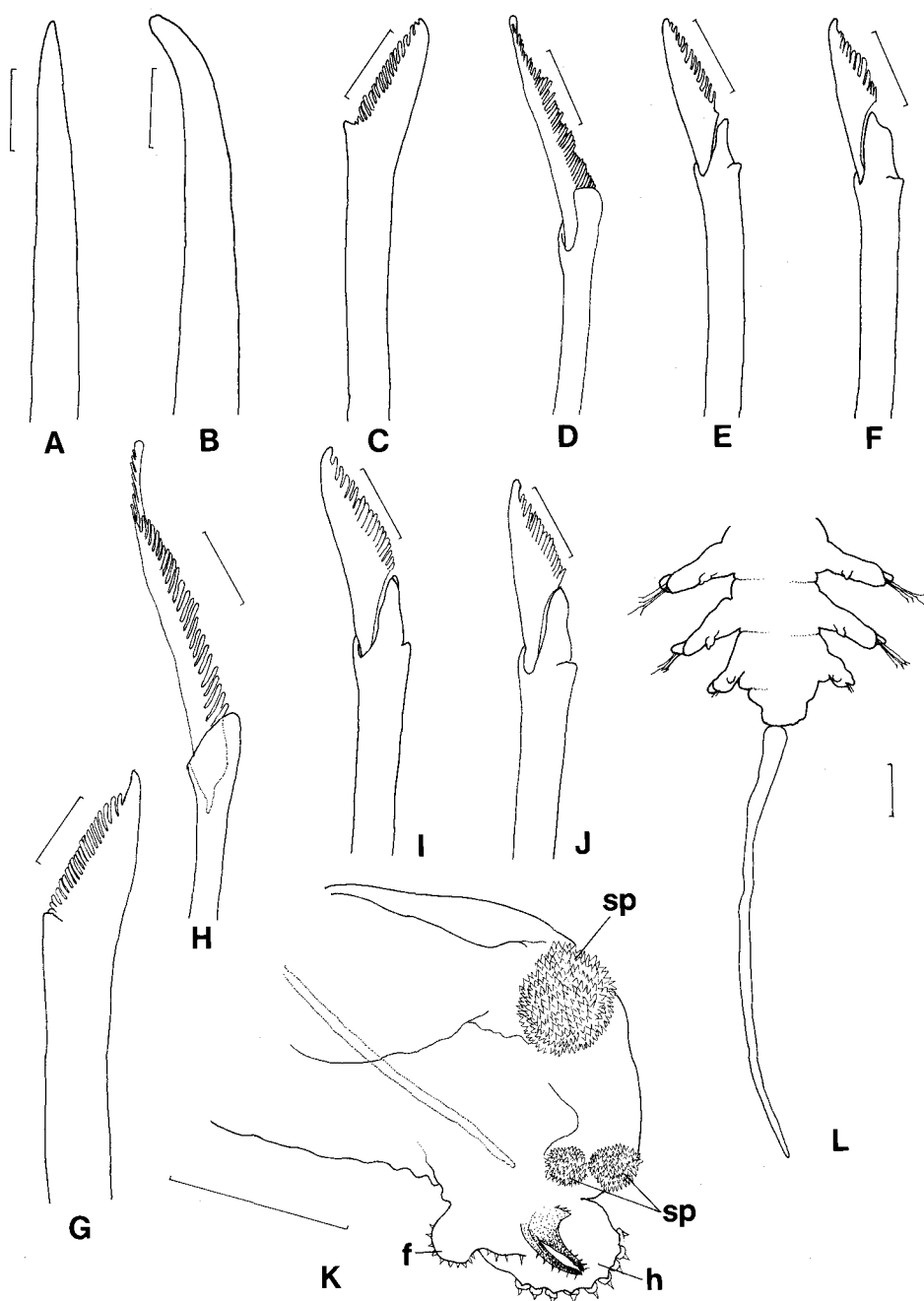


Fig. 15. *Pisione paucisetosa* sp. nov. Holotype, Iv 1407. Male. A. Notoaciculum (33rd setiger); B. Neuroaciculum (33rd setiger); C. Supra-acicular simple seta (4th setiger); D. Long-bladed compound seta (4th setiger); E-F. Falcigers (4th setiger) from upper to lower; G. Supra-acicular simple seta (33rd setiger); H. Long-bladed compound seta (33rd setiger); I-J. Falcigers (33rd setiger) from upper to lower; K. Inner view of copulatory organ (47th setiger); L. Dorsal view of posterior end (right anal cirrus is considered to be detached). f: fan-like appendage; h: hood; sp: spinous papillae. Scale. A-J: 0.01 mm; K, L: 0.1 mm.

entire worm is rather thickened tapering only posteriorly. The paired male copulatory apparatus are conspicuous with bulging appearance on a posterior segment.

Colour:

White in alcohol. Ventral surface of posterior trunk is spotted by dark pigments.

Anterior end (Fig. 14A, B; Plate III: 3, 4):

The border of the prostomium is obscure while the anterior median groove is conspicuous. The brain extends back to the position of about 3rd setiger. One pair of eyes is located at the position of about 2nd setiger. The dorsal cirri of buccal segment are long and cirriform; the ventral cirri of the same segment are small, flask-shaped. The buccal acicula project through the skin anteriorly; their distal ends are expanded and rather truncate (Fig. 14C). The palpi are thick and long. The pharynx extends over around 4-7th setigers. The jaws are devoid of inward projection (Fig. 14D).

Parapodia (Fig. 14E, F; Plate V: 2, 3):

The ventral cirri of 1st setiger are nearly as small as those of other segments and only slightly elongated. The dorsal cirri of 2nd setiger are also short with the same appearance as those of the following segments. The presetal lobes are bilobed anteriorly; the superior lobule is digitiform with terminal pores while the inferior one is smaller and dully pointed without pores. They become single in median and posterior segments; it is spherical with dense terminal pores.

The notoacacula are straight (Fig. 15A), while the neuroacacula curve ventrally at the tip (Fig. 15B).

Setae (Fig. 15C-J; Plate VIII: 1-4):

There are one supra-acicular simple seta, one long-bladed compound seta and two falcigers on a parapodium. The distal part of the supra-acicular simple seta is obliquely truncate and serrated with about 20 teeth along the edge. The blade of the long-bladed compound seta is finely serrated with about 40 teeth; the anterior side of the distal end of the shaft stretches obliquely and forms the anterior distal plate which covers the cutting side of the blade and turns to the opposite side. The falcigers are provided with about 10-20 teeth on a blade.

Copulatory apparatus (Fig. 15K; Plate X: 7, 8):

A male bears a single pair of copulatory apparatus in posterior region of the body, between 40-54th setigers (Table 6). The apparatus is a bulging structure formed by fusion of the parapodial stem and the copulatory organ proper; it is supported by an embedded, arched aciculum; setae are completely reduced; the dorsal cirrus remains unmodified while the ventral cirrus is not recognized. The copulatory organ projects ventrally ending in a hood ornamented with about 10 terminal, wrinkled ridges each of which is distally provided with a stiff spine; the penis, whose detailed structure is unrevealed, is presumed to be retractile surrounded by the hood. A fan-like appendage projects anteriorly from inside of the basal part of the hood; it is provided with stiff cuticular hairs which are also spread on the inner surface of the organ. A large, circularly rimmed mass of spinous papillae develops posteriorly on the inner surface of the copulatory organ; in addition, two, smaller masses are deposited closely to each other below the former, just above the hood.

Posterior end (Fig. 15L):

The pygidium tapers posteriorly bearing a pair of slender anal cirri.

Remarks

The male copulatory apparatus of the present material is closely related to that of *P. gopalai vannifera* subsp. nov. only differing in the possession of two additional spinous papillae in the former. However, the two forms are clearly distinct in the setal arrangement and the shape of the pygidium; the falcigers are always two in the former though three in the latter, hence the name "*paucisetosa*"; caudal gland represented by the two subspecies of *P. gopalai* is absent in the present material.

Pisione umbraculifera sp. nov.

Material. Three male and one sexually undetermined specimens were collected from the subtidal sandy bottom of 5 m deep near the mouth of Amitori Bay, northwestern part of Iriomote Island, Taketomi-cho, Yaeyama Islands (24°17'46"N, 123°40'11"E), subtropical archipelago of southwestern Japan, on April 23rd, 1995. Type series are designated as shown in Table 7.

Table 7. Body size and position of male copulatory apparatus in *Pisione umbraculifera* sp. nov.

Sex	Body length (mm)	Number of setigers	Copulatory apparatus	Registr. No.(Iv)	Remarks
male	4.0	33	30–32nd	1423	holotype
?	13.7	80	absent	1424	paratype
male	7.7	67	32–34th	1425	paratype, SEM
male	4	succeeding	segments	1426	paratype, SEM

Diagnosis: Body length up to 13.7 mm. Prostomium distinct. Buccal segment characteristic of the genus. Ventral cirri of 1st setiger longer than the parapodial stem of the same segment. Dorsal cirri of 2nd setiger small, flask-shaped. Presetal lobes bilobed anteriorly and single posteriorly. One obliquely truncate supra-acicular simple seta, one long-bladed compound seta with anterior distal plate and three falcigers on a parapodium. Male copulatory apparatus in a short series on some posterior segments; parapodial stems and setae of the segment unmodified, while ventral cirri elongated. Copulatory organ proper forming a terminal spiral covered with an umbrella-like cuticular plate posteriorly, a subterminal knob near the penis, and a bulge in the center of the spiral part; another digital process projecting outwards at the lateral side of the spiral; a short, digital process with papillae present more basally.

Holotype:

Male. Body length 4.0 mm with 33 setigers. Trunk, exclusive of parapodia, around 0.22 mm wide throughout. Length of parapodial stem around 0.15 mm throughout. Brain extending back to the position of 3rd setiger. Paired eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.12 mm long; buccal acicula 0.15 mm long; palpi 0.60 mm long; pharynx extending over 4–8th setigers. Ventral cirri of 1st setiger 0.15 mm long. Copulatory apparatus on 30–32nd setigers.

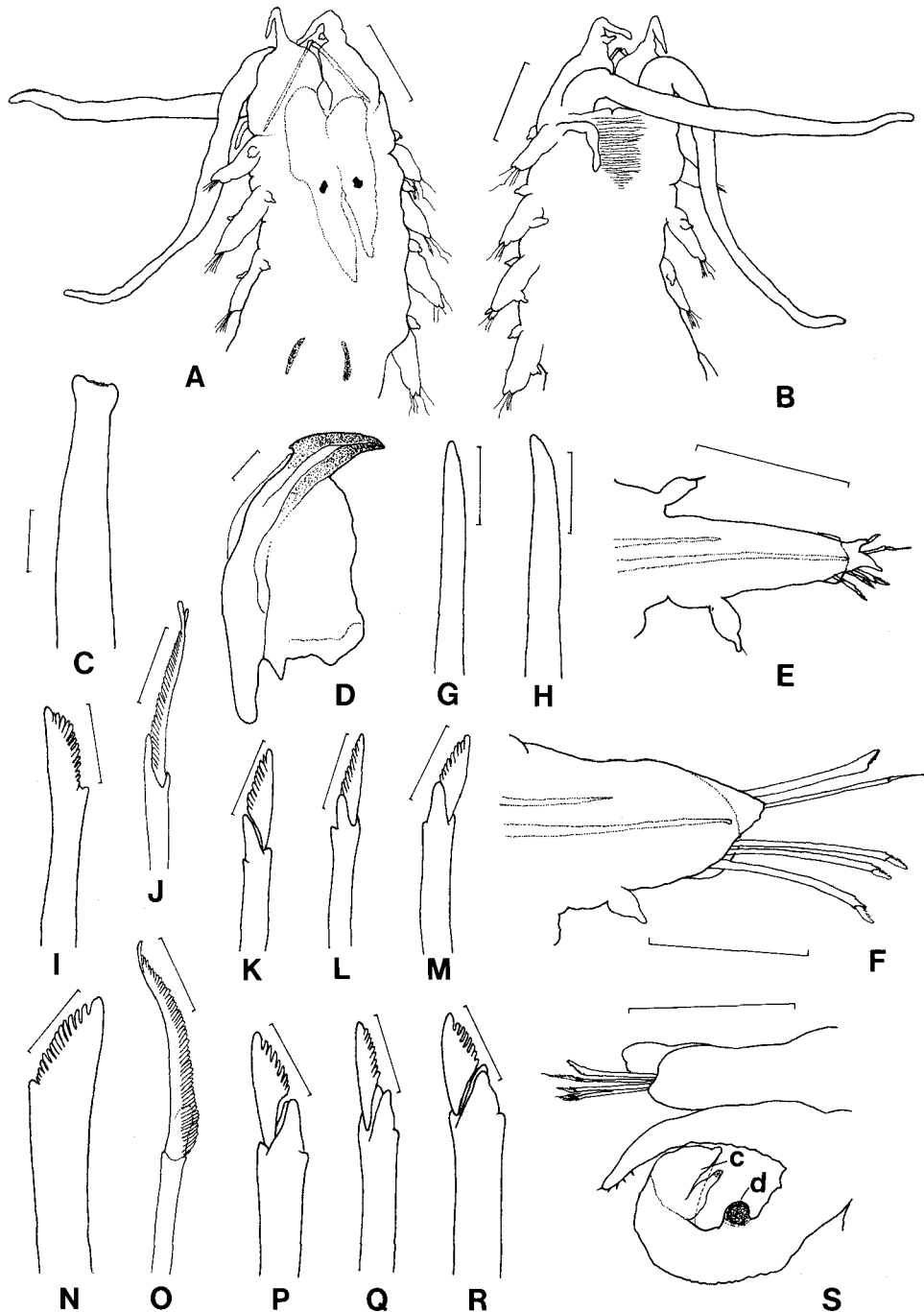


Fig. 16. *Pisione umbraculifera* sp. nov. Holotype, Iv 1423. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (4th setiger); F. Anterior view of a median parapodium (29th setiger); G. Notoaciculum (29th setiger); H. Neuroaciculum (29th setiger); I. Supra-acicular simple seta (4th setiger); J. Long-bladed compound seta (4th setiger); K-M. Falcigers (4th setiger) from upper to lower; N. Supra-acicular simple seta (29th setiger); O. Long-bladed compound seta (29th setiger); P-R. Falcigers (29th setiger) from upper to lower; S. Posterior view of a copulatory organ (31st setiger). c: cuticular plate; d: digital process. Scale. A, B, E, F, R: 0.1 mm; C, D, G-R: 0.01 mm.

Habitus (Plate I: 10):

The largest specimen measures 13.7 mm long with 80 setigers (Table 7). The proportion of the entire worm is rather thickened and log-like, not tapering posteriorly. The parapodial stem is a little shorter than the width of the same segment except for some anterior ones where they are shorter, especially those of 1st setiger is about half the width of the trunk. A series of male fertile segments is recognizable posteriorly.

Colour:

White in alcohol.

Anterior end (Fig. 16A, B; Plate III: 5, 6):

The prostomium is pentagonal and elongated. The brain extends back to the position of about 3rd setiger. One pair of eyes is located at the position of about 2nd setiger. The buccal segment slightly tapers anteriorly; its dorsal cirri are long and cirriform; the ventral cirri are small, elongated globose structure. The buccal acicula are well-developed projecting through the skin anteriorly; their distal ends are expanded (Fig. 16C). The palpi are extremely long, about five times as long as the dorsal cirri of the buccal segment. The pharynx extends over around 4–8th setigers. The jaws are devoid of inward projection (Fig. 16D).

Parapodia (Fig. 16E, F; Plate V: 4, 5):

The ventral cirri of 1st setiger are longer than the parapodial stem of the same segment. The dorsal cirri of 2nd setiger are the same shape and size as those of the following segments. Both of the dorsal and the ventral cirri of body segments are not flask-shaped, but rather spindle-shaped. The presetal lobes are bilobed anteriorly; both the superior and the inferior lobules are triangular and devoid of terminal papillae; the inferior is longer than the superior. They become single in median and posterior segments; there it is digitiform or triangular with a small number of terminal pores.

The notoacacula are straight (Fig. 16G) and the neuroacacula are also nearly straight (Fig. 16H).

Setae (Fig. 16I–R; Plate VIII: 5–9):

There are one supra-acicular simple seta, one long-bladed compound seta and three falcigers on a parapodium. The distal part of the supra-acicular simple seta is obliquely truncate and serrated with about 15 teeth along the edge. The blade of the long-bladed compound seta is finely serrated with more than 30 teeth; the anterior side of the distal end of the shaft stretches obliquely towards the edge of the blade forming the anterior distal plate over the basal part of the blade. The serration of the blades of falcigers are coarse with less than 10 teeth on a blade.

Copulatory apparatus (Fig. 16S; Plate XI: 1–3):

Male copulatory apparatus are located on three or four succeeding segments starting from 30–32nd setiger (Table 7). The ventral cirri of these segments are modified and elongated as thick, tapering processes nearly as long as the parapodial stem; they are situated in front of the copulatory organ and project ventrally; the surface is smooth and scarce of palpocils. The parapodial stems, the setae and the dorsal cirri remain unmodified there. The copulatory organ proper arises from the thick base of the parapodial stem ventro-laterally and elongates; it once twists anteriorly to form a spiral subterminally and ends in the cuticular penis. A wide, umbrella-like cuticular plate which is hung from the main stem

of the copulatory organ covers the spiral part. A bulge is recognized at the center of the spiral part. Another digital process projects outwards at the lateral side of the spiral. More basally, at the median part of the copulatory organ, arises ventrally a short, thick digital process whose end is protrusile and covered with papillae.

Posterior end:

The posterior end appears to be truncate; the pygidium is short; the anal cirri has not been observed.

Remarks

The combination of characters such as the elongated ventral cirri of 1st setiger, the small dorsal cirri of 2nd setiger, the presence of the long-bladed compound setae and the absence of the infra-acicular simple setae in the present material is common to *P. alikunhii* Tenerelli, 1965, *P. galapagoensis* Westheide, 1974, *P. laubieri* Hartmann-Schröder, 1970, *P. martinsi* Hartmann-Schröder, 1974, *P. parhelenae* De Wilde & Govaere, 1995, *P. primitiva* De Wilde & Govaere, 1995, *P. parhelenae* De Wilde & Govaere, 1995, *P. papuensis brevis* subsp. nov. and *P. bulbifera* sp. nov. in the genus. They can be distinguished from each other by comparing their male copulatory apparatus. The parapodial stems of the male fertile segments are more or less modified or reduced in most of these species; both the parapodial stems and the setae remain unmodified only in *P. helenae*, *P. primitiva*, *P. bulbifera* and the present form. *P. primitiva* and *P. bulbifera* are distinguished from the present material in the absence of cuticular plate on the copulatory organ proper. *P. helenae* which bear cuticular plate on the copulatory organ is distinguished from the present material in the form of ventral cirrus of copulatory segments which is digitate with a secondary process. The detailed structure of the male copulatory organ, especially of the umbrella-like cuticular plate, is peculiar to the present form. Therefore, it is erected here as a new species whose name is derived from the possession of the umbrella-like plate.

***Pisone vestigialis* sp. nov.**

Material. Six male, seven female and eight sexually undetermined specimens were collected from water's edges of two exposed beaches of very coarse sand or granule, located in the cool temperate region of east coast of Honshu, Japan: Kirikiri, Otsuchi-cho, Iwate Prefecture (39°22'15"N, 141°57'26"E) and Miyato-jima, Naruse-cho, Miyagi Prefecture (38°19'25"N, 141°09'50"E). Type series is designated as shown in Table 8.

Diagnosis: Body length up to 24.3 mm. Prostomium distinct. Buccal segment characteristic of the genus. Ventral cirri of 1st setiger longer than the parapodial stem of the same segment. Dorsal cirri of 2nd setiger small, flask-shaped or only slightly elongated. Presetal lobes sub-bilobed with a minute inferior lobule. One obliquely truncate supra-acicular simple seta, and four falcigers on a parapodium; an infra-acicular simple seta may replace the uppermost falciger in males. Male copulatory apparatus on some posterior segments in a series; their parapodial stems and setae unmodified; ventral cirri elongated. Copulatory organ proper double-stemmed, forming a terminal spiral provided with a sheath-like arc surrounding the penis; a triangular, cuticular plate standing in front of the spiral.

Holotype:

Male. Body length 15.9 mm with 133 setigers. Trunk usually exceeding 0.3 mm in width exclusive of parapodia. Parapodial stem around 0.15 mm long except for that of

Table 8. Body size, and position of fertile segments and infra-acicular simple setae in *Pisone vestigialis* sp. nov. "Fertile segments" denotes setigers with copulatory apparatus for male and those with ova for female, respectively.

Sex	Body length (mm)	No. setigers	Fertile segments	Infra-acicular simple setae	Date of collection	Locality	Registr. No.(Iv)	Remarks
male	15.9	133	68-93rd	28-119th; 23-114th	1991-V-16	Kirikiri	1427	holotype
male	15.8	100	60-68th	18-92nd	1994-V-10	Kirikiri	1430	paratype
male	12.6	94	54-64th	13-79th	1994-V-10	Kirikiri	1431	paratype
male	17.4	112	49-60th	19-101st	1983-V-19	Kirikiri	1436	paratype
male	8.9	77	49-56th	34-66th; 44-64th	1982-VII-10	Miyato	1439	
male	> 7.6	> 75	55-61st	33-59th; 32-74th	1982-VII-10	Miyato	1440	SEM
female	7.9	45	25-44th	absent	1991-V-16	Kirikiri	1428	paratype
female	24.3	131	30-125th	absent	1994-V-10	Kirikiri	1432	paratype
female	12.7	95	33-95th	absent	1994-V-10	Kirikiri	1433	paratype
female	14.7	95	21-95th	absent	1990-V-26	Kirikiri	1434	paratype
female	14.3	88	22-81st	absent	1990-V-26	Kirikiri	1435	paratype
female	> 9.7	> 55	28-55th	absent	1981-V-23	Kirikiri	1437	paratype
female		> 34	21-34th	absent	1981-V-23	Kirikiri	1438	paratype, SEM
?	14.6	85	absent	33-44th; 41-42nd	1991-V-16	Kirikiri	1429	paratype
?	10.8	86	absent	absent	1982-VII-10	Miyato	1441	
?	10.8	83	absent	21-57th; 30-81st	1982-VII-10	Miyato	1442	
?	9.6	78	absent	14-71st; 16-77th	1982-VII-10	Miyato	1443	
?	9.0	73	absent	absent	1982-VII-10	Miyato	1444	
?	7.7	71	absent	absent	1982-VII-10	Miyato	1445	
?	8.6	70	absent	36-57th; 26-55th	1982-VII-10	Miyato	1446	
?	8.7	62	absent	23-59th; 37-57th	1982-VII-10	Miyato	1447	

1st setiger with 0.08 mm long. Brain extending back to the position of 3rd setiger. Paired eyes located at the position of 2nd setiger. Dorsal cirri of buccal segment 0.25 mm long; buccal acicula 0.14 mm long; palpi 0.50 mm long; pharynx extending over 4-7th setigers. Ventral cirri of 1st setiger 0.20 mm long. Infra-acicular simple setae in the range of 28-119th setigers on the right and 23-114th on the left. Copulatory apparatus on 68-93rd setigers.

Habitus (Plate I: 11):

Body length attains 24.3 mm; the maximal number of setigers is 133 (Table 8). The shape of the entire worm is slender and gradually tapers posteriorly. The trunk is apparently wider on fertile segments in both sexes. The length of the parapodial stems, except for that of 1st setiger which is much shorter (about 0.1 mm), is nearly half the width of the trunk from which it arises.

Colour:

White in alcohol. The ova are green in fresh material.

Anterior end (Fig. 17A, B; Fig. 19A, B; Plate III: 7, 8):

The prostomium is pentagonal or diamond-shaped. The brain extends to the position of about 3rd setiger. One pair of eyes is located at the position of about 2nd setiger. The dorsal cirri of buccal segment are long and cirriform; the ventral cirri are small, flask-shaped. The buccal acicula are well-developed projecting through the skin anteriorly; their distal ends are expanded and truncate (Fig. 17C; Fig. 19C). The palpi are thick

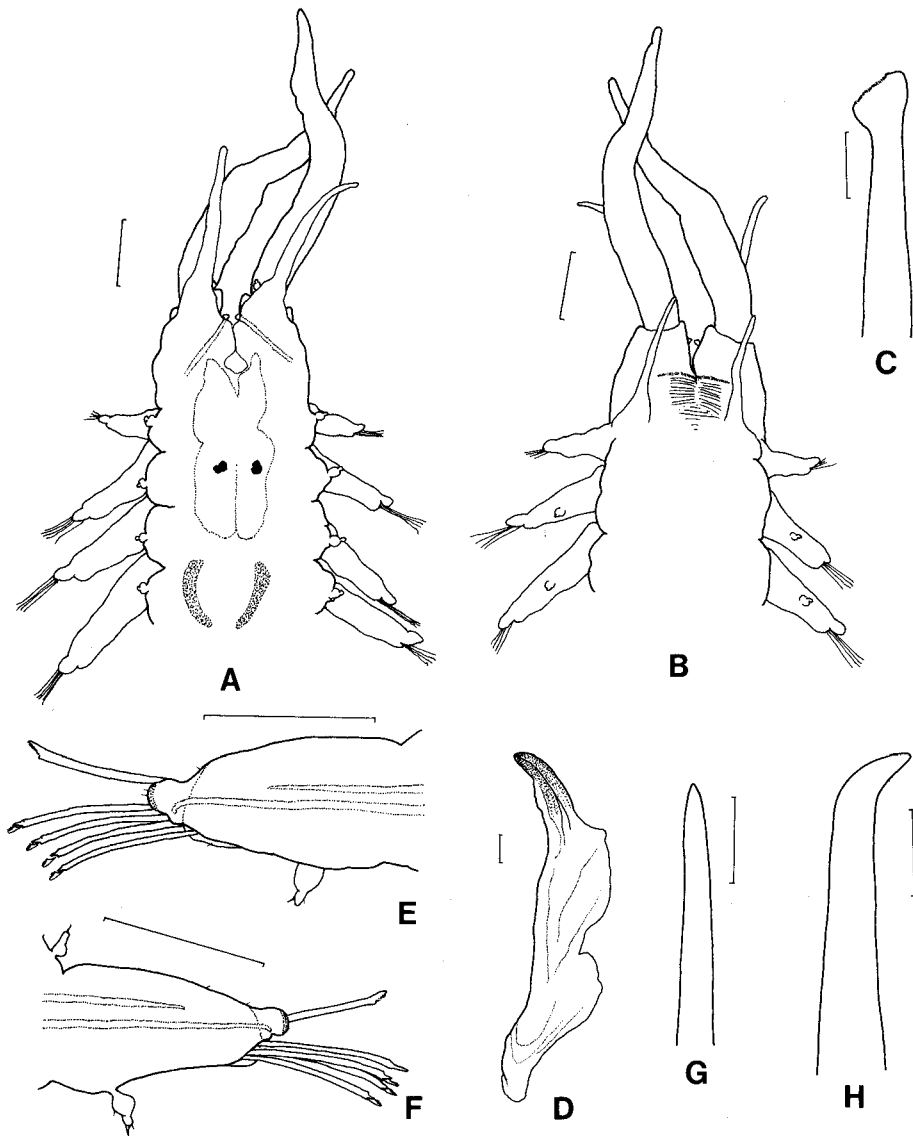


Fig. 17. *Pisione vestigialis* sp. nov. Holotype, Iv 1427. Male. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (6th setiger); F. Anterior view of a median parapodium (65th setiger); G. Notoaciculum (64th setiger); H. Neuroaciculum (64th setiger). Scale. A, B, E, F: 0.1 mm; C, D, G, H: 0.01 mm.

and long, about twice as long as the dorsal cirri of the buccal segment. The pharynx extends over around 4–7th setigers. The jaws are devoid of inward projection (Fig. 17D; Fig. 19D).

Parapodia (Fig. 17E, F; Fig. 19E, F; Plate V: 6):

The ventral cirri of 1st setiger are elongated and longer than the parapodial stem of the same segment. The dorsal cirri of 2nd setiger are small, flask-shaped being the same as those on the following segments; in some specimens, they appear to be only slightly elongated. The presetal lobes are spherical and bear numerous terminal pores; close

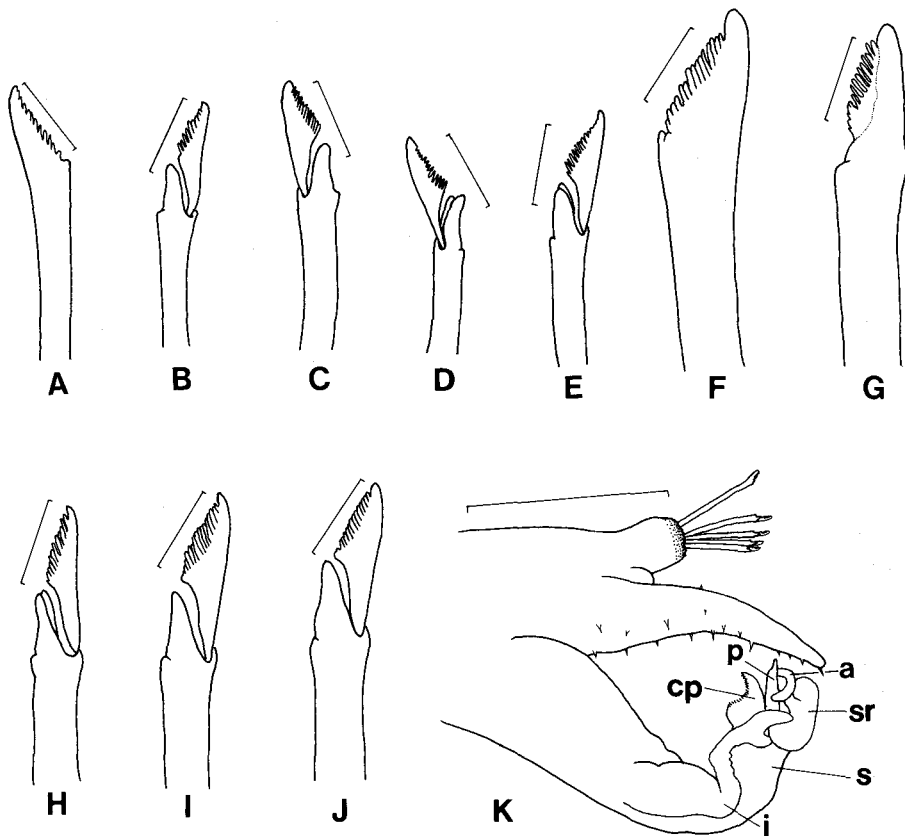


Fig. 18. *Pisone vestigialis* sp. nov. Holotype, Iv 1427. Male. A. Supra-acicular simple seta (3rd setiger); B. Uppermost falciger (3rd setiger); C-E. 2nd, 3rd and lowermost falcigers (4th setiger); F. Supra-acicular simple seta (65th setiger); G. Infra-acicular simple seta (65th setiger); H. Uppermost falciger (65th setiger); I. Median falciger (64th setiger); J. Lowermost falciger (64th setiger); K. Anterior view of a copulatory organ (89th setiger). a: sheath-like arc; cp: cuticular plate; i: inferior stem; p: penis; s: superior stem; sr: spiral part. Scale. A-J: 0.01 mm; K: 0.1 mm.

examination has revealed that the presetal lobes are sub-bilobed, accompanied inferiorly by a minute, vestigial lobule.

The notoacacula are straight (Fig. 17G; Fig. 19G), while the neuroacacula curve ventrally at the tip (Fig. 17H; Fig. 19H).

Setae (Fig. 18A-J; Fig. 20A-J; Plate VIII: 10-18):

There are usually one supra-acicular simple seta and four falcigers on a parapodium. An infra-acicular simple seta may replace the uppermost falciger. So far as the specimens are examined, the infra-acicular simple setae never appear in females while all the males with copulatory apparatus possessed them (Table 8); when present, they are located irregularly on some of the setigers except for those near both ends. The distal part of the supra-acicular simple setae is obliquely truncate and serrated with about 15 teeth along the edge. The infra-acicular simple setae are also provided with shallow serration with about 15 teeth on the concave side followed by a subterminal notch; the opposite side is convex forming a

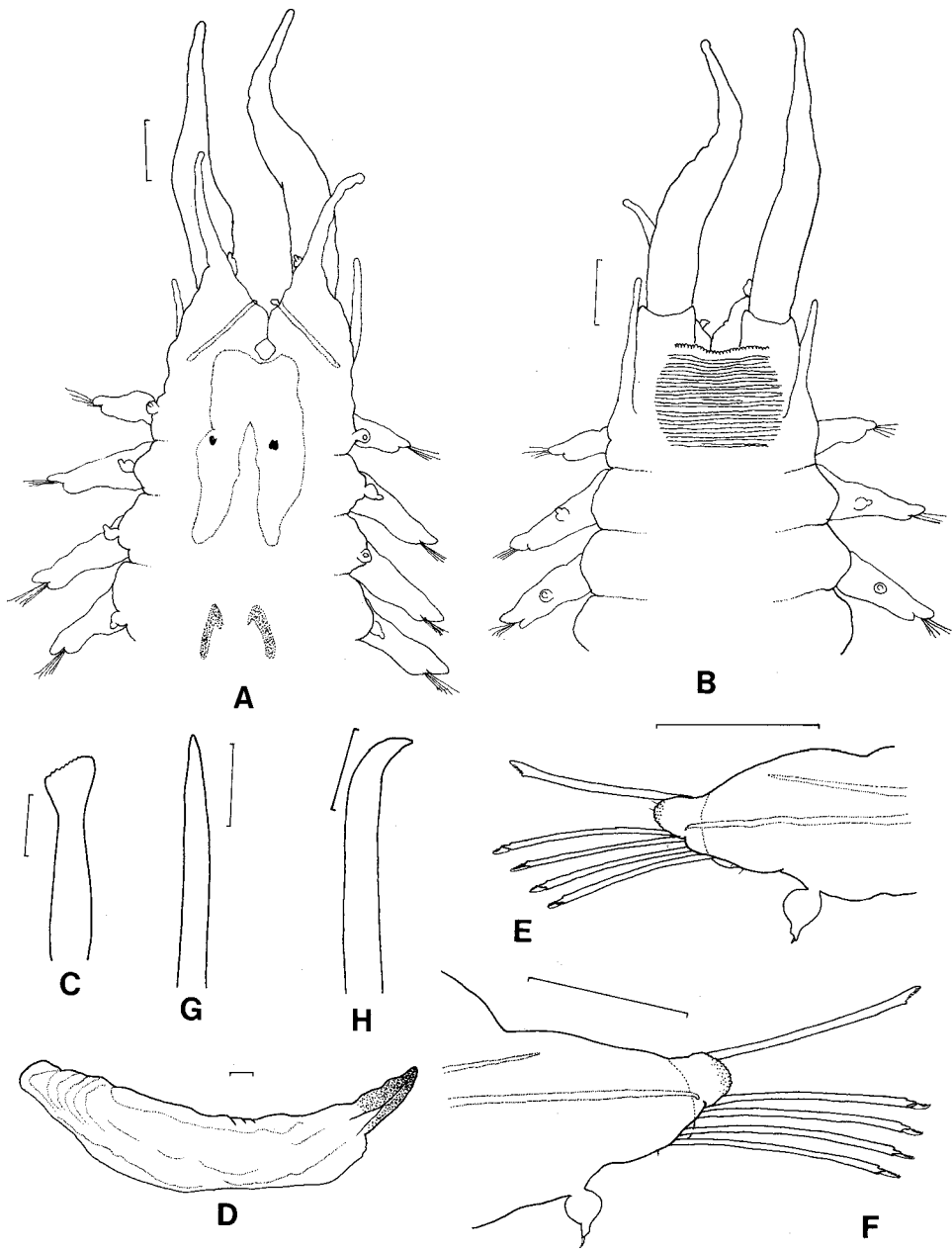


Fig. 19. *Pisone vestigialis* sp. nov. Paratype, Iv 1432. Female. A. Dorsal view of anterior end; B. Ventral view of anterior end; C. Buccal aciculum; D. Jaw; E. Anterior view of an anterior parapodium (5th setiger); F. Anterior view of a median parapodium (31st setiger); G. Notoaciculum (58th setiger); H. Neuroaciculum (38th setiger). Scale. A, B, E, F: 0.1 mm; C, D, G, H: 0.01 mm.

blunt angle. The falcigers are provided with about 15 teeth, at least more than 10 on a blade.

Copulatory apparatus (Fig. 18K; Plate XI: 4–6):

The male copulatory apparatus are arranged consecutively starting from 49–68th setiger

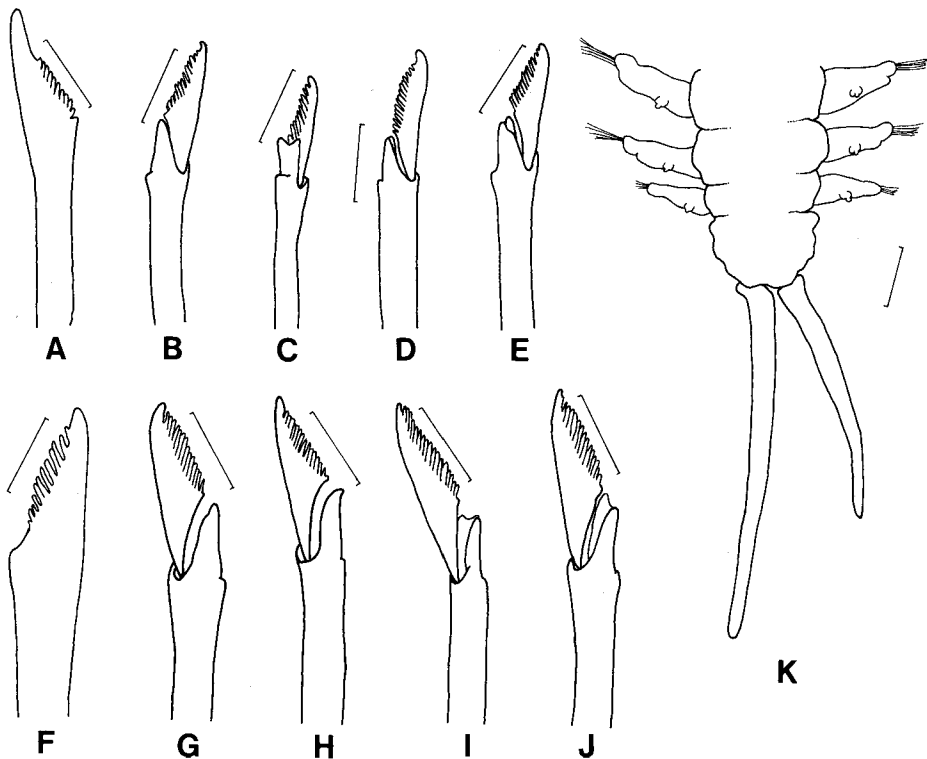


Fig. 20. *Pisone vestigialis* sp. nov. Paratype, Iv 1433. Female. A. Supra-acicular simple seta (5th setiger); B-E. Falcigers (5th setiger) from upper to lower; F. Supra-acicular simple seta (38th setiger); G-J. Falcigers (38th setiger) from upper to lower; K. Ventral view of posterior end. Scale. A-J: 0.01 mm; K: 0.1 mm.

and continue to 56–93rd (Table 8). The ventral cirri of these segments are modified and elongated as thick, tapering processes nearly as long as the parapodial stems; they project ventrally in front of the copulatory organ, and are provided with many palpocils. The parapodial stem, the setae and the dorsal cirri remain unmodified there. The copulatory organ proper arises from the thick base of the parapodial stem ventro-laterally and elongates; it is divided into double stems near the base, the superior stem and the inferior stem; both stems project laterally keeping connection by a thin membrane with each other. The superior stem in which the sperm duct is carried turns upwards and twists anteriorly to form a spiral; its end is strengthened by a cuticular process forming a penis. The inferior stem is bifid at its end. A sheath-like arc arises from the outer margin of the spiral part of the superior stem and surrounds the penis from above. A triangular, cuticular plate whose outer margin is ornamented with numerous fine wrinkles erects from the superior stem and covers the spiral region anteriorly. A small, pointed lobule projects on the outer margin of the spiral just near to the base of the arc. One of the bifid ends of the inferior stem attaches to the base of the cuticular plate, and the other to the base of the spiral region.

Ovary:

In mature females, the ovary are observed in a large number of succeeding segments from 21st–33rd to nearly the end of body (Table 8).

Posterior end (Fig. 20K):

The pygidium tapers posteriorly bearing a pair of slender anal cirri though detached off in the holotype.

Remarks

P. remota Southern, 1914 and the present species are alike in most characters except for the details of male copulatory apparatus, for example, the inferior stem of the former is developed so weakly that it cannot reach the superior stem terminally.

The present species is judged to be very closely related to *P. crassa* Yamanishi, 1976 on account of their striking similarities in the structure of the male copulatory apparatus. They can be distinguished only by the shape of cuticular appendage in front of the spiral which is a triangular plate in the present material whereas it is provided with a spherical swelling terminally in *P. crassa* (Yamanishi, 1991). The two, however, differ in other characters: dorsal cirri of 2nd setiger are elongated, buccal acicula are very weak, and acicular simple setae are absent in *P. crassa*.

As it has not been recorded in any other species of the genus, the sub-bilobed presetal lobe is considered to be peculiar to the present species; the new name comes from the vestigial condition of this lobule.

Discussion

Validity of species and subspecies:

Among the 30 reported species of the genus *Pisone*, *P. contracta* Ehlers, 1901 and *P. germanica* Augener, 1924 have so far been synonymized with *P. oerstedii* and *P. remota*, respectively (Hartman, 1939). Thus 28 species and one subspecies have been treated as valid. As results of the present study, five new species and three new subspecies are added, and *P. oerstedii pulla* is treated as a distinct species as discussed in the systematic account of *P. mista* (p. 113). As shown below, *P. tortuosa* is regarded as an invalid species. Accordingly 33 species accompanied by three subspecies can be regarded as valid at present (Table 9).

Distribution of main diagnostic characters in the genus is presented in Table 10. A working key to the species and the subspecies of the genus is also given as an appendix. Not all of these species, however, have been fully described. For example, *P. longipalpa* can be defined only by the extremely elongated palpi, and *P. reducta* only by the reduced condition of cephalic appendages. Though male copulatory apparatus is essentially important in the classification of closely related forms, they are left unknown in *P. oerstedii*, *P. longipalpa*, *P. reducta*, *P. corallicola*, *P. pulla*, *P. levisetosa* and *P. mista*; detailed description of the apparatus has not yet been given for *P. koepkei*, *P. laubieri*, *P. martinsi* and *P. papillata*. Further, little attention has been paid on the parapodial structure and shape of setae in the three Indian species, *P. gopalai*, *P. complexa* and *P. alikunhui*, though their copulatory apparatus were treated with considerable detail.

P. tortuosa from South Australia was erected as a new species based on the differences in the body length, the shape of the distal margin of the buccal acicula, the location of eyes, the shape and the coloration of the parapodial acicula, and the shape of the long-bladed compound setae from the most closely allied species, *P. papillata*. It was separated from the other allied species, *P. africana*, by the difference in the shape of the elongated dorsal cirri of 2nd setiger (Hartmann-Schröder & Parker, 1990). However, the male copulatory apparatus of *P. tortuosa* has been left unknown. Except for the difference in the shape of the long-bladed compound setae which might be of some taxonomical significance, all these characters are attributable to individual variations or mere shrinkage by fixation. It is,

therefore, hardly acceptable to regard *P. tortuosa* as a distinct species.

P. laubieri consists of two forms, the smaller being less than 4 mm in body length with a pair of male copulatory apparatus on about 12th setiger, and the larger being more than 4 mm with 1–3 pairs of male copulatory apparatus usually on setigers posterior to the 30th (Hartmann-Schröder, 1970). According to the description, the structure of the male copulatory apparatus differs critically between these two forms. In the smaller form, the copulatory organ proper is long and tapering with some appendages whose detailed structure is unknown; the ventral cirrus is elongate, finger-like; the terminal part of the parapodial lobe remains distinct accompanied by a few setae. In the larger form, the copulatory organ is a bulging structure; the ventral cirrus and the setae are absent. It seems unlikely that these two forms belong to the same species even if the setal characters were identical. The larger form should be regarded as the representative of the present species since a specimen of 5 mm long has been designated as the holotype. The smaller form should be separated from *P. laubieri*, and reexamination of the material is needed.

P. subulata from Japan can be distinguished from *P. levisetosa* from Qingdao only by the enlargement of the notoacacula projecting through the body wall of posterior segments; they coincide exactly each other in other characters, especially, in the smooth edge of the blade of the lowermost falciger which is exclusively represented in these two forms. Therefore, they might be regarded as subspecies of a single species. At present, they are tentatively treated as separate species to wait until the male copulatory apparatus of the latter is revealed.

Characteristics of the Japanese fauna:

In addition to the five species of the genus *Pisone* so far known from Japanese waters, nine species are newly recorded in the present study (Table 11). Thus, out of the 33 species of the genus, the Japanese fauna comprises as many as 14 species. There is no other district with so many species of *Pisone* in the world. The richness of the Japanese fauna of *Pisone* is considered to be partly due to the result of extensive investigation and partly due to the diverse climatic condition of the district which involves subtropical, warm temperate and cool temperate regions.

Among the Japanese species of *Pisone*, eight species are distributed in the subtropical region. *P. africana*, *P. mista*, *P. papuensis brevis* and *P. paucisetosa* are inhabitants of intertidal sandy substrata. *P. africana* is recorded from Iriomote Island, the Ryukyu Islands; *P. mista* is from Chichi-jima, the Bonin Islands; *P. papuensis brevis* and *P. paucisetosa* are distributed both in the Ryukyu and the Bonin Islands (Yamanishi, present study and unpublished data). *P. brevicirra platycauda*, *P. bulbifera*, and *P. umbraculifera* from Iriomote Island, and *P. parva* from Chichi-jima Island, are known subtidally or from shallow water bottom. It is surprisingly interesting that the above three subtidal species from Iriomote Island were obtained from samples collected simultaneously by scuba-diving at an exactly same site in Amitori Bay. Their well-differentiated male copulatory apparatus might be permitting the sympatric occurrence of these congeneric species.

Five species are distributed in the warm temperate region. *P. gopalai vannifera* and *P. papillata* are known intertidally in the Seto Inland Sea. *P. subulata* occurs at shallow sandy bottoms of various localities in the Sea of Japan and in the Seto Inland Sea (Yamanishi, 1992 and unpublished data). *P. crassa* is a common inhabitant of coarse sand beaches (Yamanishi, 1976 and unpublished data). *P. africana* is recorded from a shallow sandy bottom of Kii Peninsula (Uchida, 1988).

Two species, *P. longipalpa* and *P. vestigialis* are distributed in the cool temperate region. The former was recorded from a depth of 918 m, off the Kuril Islands, Northwest Pacific (Uschakov, 1956). The latter is an inhabitant of intertidal sandy substrata. As

Table 9. List of the species of the genus *Pisione*.

Species	Locality	Literature
<i>oerstedii</i> Grube, 1857	Chile-Peru	Grube, 1857; Ehlers, 1901; Hartman, 1939; Hartmann-Schröder, 1962
<i>remota</i> Southern, 1914	North Sea, Mediterranean	Southern, 1914; Tenerelli, 1965; Stecher, 1968
<i>gopalai gopalai</i> Alikunhi, 1941	Madras	Alikunhi, 1941
<i>complexa</i> Alikunhi, 1947	Madras	Alikunhi, 1947
<i>puzae</i> Siewing, 1953	Mediterranean	Siewing, 1953; Tenerelli, 1965
<i>koepkei</i> Siewing, 1955	Peru	Siewing, 1955
<i>longipalpa</i> Uschakov, 1956	Kuril Is.	Uschakov, 1956
<i>africana</i> Day, 1963	S. Africa, M. Japan	Day, 1963; Hartmann-Schröder, 1970; Uchida, 1988
<i>alikhunhii</i> Tenerelli, 1965	Madras	Alikunhi, 1951; Tenerelli, 1965
<i>reducta</i> Storch, 1967	Red Sea	Storch, 1967
<i>laubieri</i> Hartmann-Schröder, 1970	C. d'Ivoire	Laubier, 1967; Hartmann-Schröder, 1970
<i>corallicola</i> Hartmann-Schröder, 1974	Tanzania	Hartmann-Schröder, 1974a
<i>martinsi</i> Hartmann-Schröder, 1974	Angola	Hartmann-Schröder, 1974b
<i>pulla</i> Westheide, 1974	Galapagos	Westheide, 1974
<i>galapagoensis</i> Westheide, 1974	Galapagos	Westheide, 1974
<i>crassa</i> Yamanishi, 1976	M. Japan	Yamanishi, 1976; Yamanishi, 1991
<i>papillata</i> Yamanishi, 1976	M. Japan	Yamanishi, 1976
<i>hermansii</i> Svonick, 1991	California	Svonick, 1991
<i>levisetosa</i> Zhao-Jing, Westheide & Wu, 1991	Qingdao	Zhao-Jing, Westheide & Wu, 1991
<i>subulata</i> Yamanishi, 1992	M. Japan, Papua New Guinea	Yamanishi, 1992; De Wilde & Govaere, 1995
<i>papuensis papuensis</i> Govaere & De Wilde, 1993	Papua New Guinea	Govaere & De Wilde, 1993; De Wilde & Govaere, 1995
<i>helenae</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>parva</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>ungulata</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>primitiva</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>brevicirra brevicirra</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>parhelenae</i> De Wilde & Govaere, 1995	Papua New Guinea	De Wilde & Govaere, 1995
<i>hartmannschroederiae</i> Westheide, 1995	Florida	Westheide, 1995
<i>brevicirra platycauda</i> subsp. nov.	S. Japan	present study
<i>gopalai vannifera</i> subsp. nov.	M. Japan, Australia	present study
<i>papuensis brevis</i> subsp. nov.	S. Japan	present study
<i>bulbifera</i> sp. nov.	S. Japan	present study
<i>mista</i> sp. nov.	S. Japan	present study
<i>paucisetosa</i> sp. nov.	S. Japan	present study
<i>umbraculifera</i> sp. nov.	S. Japan	present study
<i>vestigialis</i> sp. nov.	N. Japan	present study

shown in the systematic account (p.127), *P. vestigialis* is more closely related to *P. crassa* which is distributed in the adjacent, warm temperate region of Japan than to any other species of the genus. These are considered to be sister species and to have diverged through adaptation to different climatic conditions.

Table 10-1. Distribution of main diagnostic characters in the genus *Pisone* (to be continued).

Organs	Character	<i>afr</i>	<i>ali</i>	<i>br-br</i>	<i>br-pl</i>	<i>bul</i>	<i>com</i>	<i>cor</i>	<i>cra</i>	<i>gal</i>	<i>go-go</i>	<i>go-va</i>	<i>har</i>	<i>hel</i>	<i>her</i>	<i>koe</i>	<i>lau</i>	<i>lev</i>	<i>lon</i>
Size	Maximal number of setigers	137	52	28	43	60	100	>12	105	68	50	57	75	53	117	?	57	48	70
	Maximal body length (mm)	20.4	10.0	2.8	4.2	7.2	25.0	>1.4	24.0	14.0	10.0	8.8	8.0	8.7	35.0	17.0	5.0	8.5	17.0
	Maximal body width (mm)	0.3	?	0.06	0.16	0.20	0.23	0.34	0.8	0.27	0.18	0.25	0.2	0.29	0.9	?	?	0.25	0.25
Prostomium	Distinct prostomium	+	+	+	-	+	+	+	+	+	-	+	+	+	+	+	+	+	+
Buccal segment	Buccal acicula	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+
Proboscis	Inward projection of jaws	-	-	?	+	-	-	-	-	-	-	-	?	?	-	+	-	-	-
Parapodium	Elongation of ventral cirri of 1st setiger	+	+	-	-	+	-	-	+	+	-	-	+	+	+	-	-	+	+
	Elongation of dorsal cirri of 2nd setiger	+	-	-	-	-	-	-	+	-	-	-	+	-	+	-	-	-	-
	Bilobed presetal lobe	+	?	+	+	±	?	+	-	-	-	±	-	±	-	-	-	-	-
	Notoacicula projecting through skin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Seta	Infra-acicular simple setae	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+
	Long-bladed compound setae	+	+	-	-	+	+	+	-	+	+	+	+	+	-	+	+	+	-
Copulatory organ	Fusion of copulatory organ and parapodial lobe	-	±	-	-	-	+	?	-	±	+	+	-	-	-	?	+	?	?
	Spiral structure	-	-	+	+	-	-	?	+	-	-	-	-	-	+	?	-	?	?
	Inferior stem derived from bidigitate process	-	-	-	-	-	-	?	+	-	-	-	-	-	+	-	-	?	?
	Bidigitate process homologous to inferior stem	-	-	+	+	-	-	?	-	-	-	-	-	-	-	?	-	?	?
	Sheath-like arc	-	-	-	-	-	-	?	+	-	-	-	-	-	+	?	?	?	?
	Cuticular plate	-	-	-	-	-	-	?	+	-	-	-	+	+	+	?	?	?	?
	Elongated ventral cirrus	+	-	+	+	+	-	?	+	+	-	-	+	+	+	+	-	?	?
	Hooded structure	-	-	-	-	-	-	?	-	-	+	+	-	-	-	-	?	?	?
	Spinous papillae	-	-	-	-	-	-	?	-	-	+	+	-	-	-	?	?	?	?
	Fan-like appendage	-	-	-	-	-	-	?	-	-	-	+	-	-	-	-	?	-	?

± marks on the line of "bilobed presetal lobe" mean "bilobed anteriorly while single lobed posteriorly".

Other ± marks show intermediate conditions.

Abbreviations of species names. *afr*: *africana*, *ali*: *alikhunhi*, *br-br*: *brevicirra brevicirra*, *br-pl*: *brevicirra platycauda*, *bul*: *bulbifera*, *com*: *complexa*, *cor*: *corallicola*, *cra*: *crassa*, *gal*: *galapagoensis*, *go-go*: *gopalai gopalai*, *go-va*: *gopalai vannifera*, *har*: *hartmannschroederiae*, *hel*: *helenae*, *her*: *hermansii*, *koe*: *koepkei*, *lau*: *laubieri*, *lev*: *levisetosa*, *lon*: *longipalpa*.

All the Japanese species of *Pisone*, except for *P. africana* which has been recorded both from subtropical and warm temperate regions, are restricted to any one of the climate regions.

Concerning the worldwide distribution of the Japanese species, *P. africana*, discovered from South Africa (Day, 1963), is expected to be widely distributed along Indo-Pacific coasts. In the present study, *P. gopalai* from South Australia (Hartmann-Schröder & Parker, 1990) is revealed to be identical with *P. gopalai vannifera* from Japan at subspecies level (p.101). Both occur in temperate regions, one in the southern and the other in the northern hemisphere. It should be noted, however, that between the two localities, *P. gopalai gopalai* is distributed in a tropical coast of the Indian Ocean, Madras (Alikunhi, 1941). It seems

Table 10-2. Distribution of main diagnostic characters in the genus *Pisione* (continued).

Organs	Character	mar	mis	oer	pa-pa	pa-br	papi	parh	parv	pau	pri	pul	puz	red	rem	sub	umb	ung	ves
Size	Maximal number of setigers	>23	121	210	78	104	95	39	29	76	>45	>59	73	?	85	64	80	>39	133
	Maximal body length (mm)	>2.5	24.9	118.0	6.0	20.3	7.6	3.4	3.0	11.6	>8.8	>4.0	24.0	?	22.0	11.2	13.7	>8.2	24.3
	Maximal body width (mm)	0.1	1.4	2.5	0.46	>0.3	?	0.15	0.17	0.3	0.28	1.2	?	0.25	1.0	0.29	0.22	0.5	>0.3
Prostomium	Distinct prostomium	+	+	-	+	+	+	+	-	-	+	-	+	-	+	+	+	+	+
Buccal segment	Buccal acicula	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+
Proboscis	Inward projection of jaws	-	-	?	-	-	-	?	+	-	?	-	+	+	-	-	-	?	-
Parapodium	Elongation of ventral cirri of 1st setiger	+	+	+	+	+	+	+	-	-	+	+	+	-	+	+	+	+	+
	Elongation of dorsal cirri of 2nd setiger	-	+	+	+	-	+	-	-	-	-	+	-	-	-	-	-	+	-
	Bilobed presetal lobe	-	+	-	-	-	+	±	+	±	±	+	-	-	±	-	±	+	-
	Notoacicula projecting through skin	-	+	-	-	-	-	-	-	-	+	-	-	-	-	+	-	+	-
Seta	Infra-acicular simple setae	-	+	-	-	-	-	-	-	-	-	-	+	-	+	+	-	-	+
	Long-bladed compound setae	+	+	-	+	+	+	+	-	+	+	+	-	-	-	+	+	+	-
Copulatory organ	Fusion of copulatory organ and parapodial lobe	±	?	?	±	±	+	+	+	+	-	?	-	?	-	-	-	-	-
	Spiral structure	?	?	?	+	+	-	-	-	-	-	?	+	?	+	-	+	-	+
	Inferior stem derived from bidigitate process	-	?	?	-	-	-	-	-	-	-	?	-	?	-	-	-	-	+
	Bidigitate process homologous to inferior stem	-	?	?	-	-	-	-	-	-	-	?	+	?	+	-	-	-	-
	Sheath-like arc	-	?	?	-	-	-	-	-	-	-	?	?	?	+	-	-	-	+
	Cuticular plate	-	?	?	-	-	-	-	-	-	-	?	?	?	+	-	+	-	+
	Elongated ventral cirrus	+	?	?	-	-	-	-	-	-	+	?	+	?	+	+	+	+	+
	Hooded structure	-	?	?	-	-	-	?	+	+	-	?	-	?	-	-	-	-	-
	Spinous papillae	?	?	?	+	-	+	-	-	+	-	?	-	?	-	-	-	-	-
	Fan-like appendage	-	?	?	-	-	?	-	-	+	-	?	-	?	-	-	-	-	-

± marks on the line of "bilobed presetal lobe" mean "bilobed anteriorly while single lobed posteriorly".

Other ± marks show intermediate conditions.

Abbreviations of species names. *mar*: *martinsi*, *mis*: *mista*, *oer*: *oerstedii*, *pa-pa*: *papuensis papuensis*, *pa-br*: *papuensis brevis*, *papi*: *papillata*, *parh*: *parhelenae*, *parv*: *parva*, *pau*: *paucisetosa*, *pri*: *primitiva*, *pul*: *pulla*, *puz*: *puzae*, *red*: *reducta*, *rem*: *remota*, *sub*: *subulata*, *umb*: *umbraculifera*, *ung*: *ungulata*, *ves*: *vestigialis*.

to be difficult to explain how such an amphi-equatorial pattern of distribution was established. It is likely that *P. parva*, which was discovered from Papua New Guinea (De Wilde & Govaere, 1995) and secondly recorded from the Bonin Islands in the present study, is widely distributed in the tropical and subtropical waters of the Pacific. *P. subulata* was also recorded from Papua New Guinea (Wilde & Govaere, 1995), though in Japan it is restricted to the temperate region. *P. papuensis* and *P. brevicirra*, both from subtropical region of Japan, are distributed in Papua New Guinea (Govaere & De Wilde, 1993; De Wilde & Govaere, 1995) though differentiated at subspecies level. All other species are, at present, endemic to Japan.

Table 11. Distribution of the Japanese species of *Pisone* and their habitats.

Species	Distribution	Climatic condition	Habitat
<i>longipalpa</i> Uschakov, 1956	Off Kuril Is.	cool temperate	bottom of 918m
<i>africana</i> Day, 1963	Ryukyu Is. Kii Peninsula	subtropical warm temperate	intertidal shallow bottom
<i>crassa</i> Yamanishi, 1976	from Honshu to Kyushu	warm temperate	intertidal
<i>papillata</i> Yamanishi, 1976	Seto Inland Sea	warm temperate	intertidal
<i>subulata</i> Yamanishi, 1992	Japan Sea Seto Inland Sea	warm temperate warm temperate	shallow bottom shallow bottom
<i>parva</i> De Wilde & Govaere, 1995	Bonin Is.	subtropical	shallow bottom
<i>brevicirra platycauda</i> subsp. nov.	Ryukyu Is.	subtropical	subtidal
<i>gopalai vannifera</i> subsp. nov.	Seto Inland Sea	warm temperate	intertidal
<i>papuensis brevis</i> subsp. nov.	Ryukyu Is. Bonin Is.	subtropical subtropical	intertidal intertidal
<i>bulbifera</i> sp. nov.	Ryukyu Is.	subtropical	subtidal
<i>mista</i> sp. nov.	Bonin Is.	subtropical	intertidal
<i>paucisetosa</i> sp. nov.	Bonin Is.	subtropical	intertidal
<i>umbraculifera</i> sp. nov.	Ryukyu Is.	subtropical	intertidal
<i>vestigialis</i> sp. nov.	Ryukyu Is. North-East Honshu	subtropical cool temperate	subtidal intertidal

There seems to be an inclination in the genus *Pisone* that larger number of species are distributed in tropical or subtropical waters when compared with temperate waters (Table 9). It is true of the Japanese fauna as shown above. The eight subtropical species in Japan is just equal in number to that of Papua New Guinea where exhaustive investigations were recently carried out (Govaere & De Wilde, 1993, De Wilde & Govaere, 1995). As for the temperate regions, richness of the Japanese fauna, with five species in warm and two in cool, is remarkable. Only two species, *P. remota* and *P. puzae*, has hitherto been known in European waters where faunal surveys must have been conducted most sufficiently in the world.

Evolutionary aspects in pisionids:

As summarized by Åkesson (1961), many authors have referred to the relationships of the Pisionidae to other polychaete families, such as Aphroditidae (*sensu lato* = scale-worms), Nephtyidae, Phyllodocidae, Glyceridae, Hesionidae and Syllidae (Grube, 1857; Levinsen, 1887; Ehlers, 1901; Southern, 1914; Hartman, 1939; Aiyar & Alikunhi, 1940; Alikunhi, 1950; Banse, 1956). Hartman (1939) pointed out that the proboscis of pisionids provided with four chitinous jaws and the terminal papillae is "clearly of the scale-worm type". Siewing (1953), who studied their innervation on adult material of *Pisone puzae*, has revealed that the dorsal cirri, the ventral cirri and the buccal acicula of the buccal segment are derived from the parapodia of 1st segment, and that their palpi are homologous not to "tentacular cirri" but to "palpi" themselves of other polychaetes. Åkesson (1961) studied the larval

morphology and histology of *Pisione remota* in detail and showed high similarity of pisionid larvae to those of aphroditids, especially of the genus *Pholoe*; the buccal segment of pisionids was detected to be formed through enlargement and torsion of the parapodial elements of 1st body segment at metamorphosis. He critically reviewed the affinities of pisionids to other families, and convincingly concluded that the family is most closely related to the Aphroditidae, especially to *Pholoe*. It is thus most reasonable to consider that pisionids have their ancestor among some *Pholoe*-like aphroditids. Reverse course that aphroditids have evolved from a pisionid is unlikely, because, as has just been referred to, the buccal segment of the Pisionidae is a highly modified structure derived from parapodia of 1st body segment.

Among the pisionid genera, *Pisionella* is considered to be most closely related to *Pholoe*: the median prostomial antenna is retained, the ventral cirri of the buccal segment are still long, and the shafts of the compound setae are serrated as in *Pholoe* (Fig. 21). In other genera, the prostomial antenna is absent, and the shafts of the compound setae are smooth. In *Pisione* and *Anoplopisione*, the ventral cirri of the buccal segment are reduced to globose structures, and the buccal acicula are present. *Anoplopisione* is distinguished from *Pisione* only by the reduced and asetigerous condition of the parapodia of the segment which corresponds to the 1st setiger of *Pisione*. In *Pisionidens*, the parapodia are more reduced and all of them are devoid of setae in adults; the ventral cirri of the buccal segment have disappeared; the buccal acicula are absent.

As regards their life form and habitat, all the pisionids are slender, agile infauna inhabiting sandy substrata, whereas species of *Pholoe* are flattened, sluggish epifauna mostly attaching hard substrata. Provided that pisionids have evolved from a *Pholoe*-like ancestor, the slender body-shape, formation of the buccal segment, and loss of the elytra in pisionids might well be explained as the results of their colonization to the high-energetic environment.

To compare pisionids with *Pholoe* in detail, the following morphological changes are considered to have been brought about in the course of evolution: extreme reduction of the prostomium, development of the buccal acicula (in *Pisione* and *Anoplopisione*), reduction of the parapodial cirri into small globose structure, inclination to elongate the dorsal cirri of 2nd setiger, reduction of the parapodia into sub-biramous type (more reduced in *Pisionidens*), development of the bilobed presetal lobes with terminal pores (at least in *Pisione*), and possession of the setae not seen in scale-worms (two types of simple setae and long-bladed compound setae).

In the genus *Pisione*, however, morphological characters thus presumed to be acquired in pisionids are not held by all the species: the buccal acicula are absent in some species; the dorsal cirri of 2nd setiger are reduced in many species; the presetal lobes are reduced to single lobed condition in many species; the lacks of the infra-acicular simple setae and of the long-bladed compound setae are frequent (Table 10). The elongated ventral cirri of 1st setiger, though not specific to pisionids but shared with *Pholoe* and other scale-worms, are also reduced in many species of *Pisione*.

Since most species of *Pisione* are extremely small-sized in polychaetes and are found exclusively from sandy habitat, they are regarded as interstitial sliders inhabiting pore spaces between sand grains, a habitat extremely limited in dimension. Then, the frequent reductions of many characters mentioned above are considered to be closely related with their small size and mode of locomotion. It has been pointed out by many authors that interstitial species prevail many polychaete families and they independently exhibit strong tendencies towards small body-size, abbreviation of appendages, or reduction of organs (Hartmann-Schröder, 1964; Laubier, 1967b; Westheide, 1971). It is highly probable, therefore, that the demand for small body size have forced the interstitial species of *Pisione* to reduce or

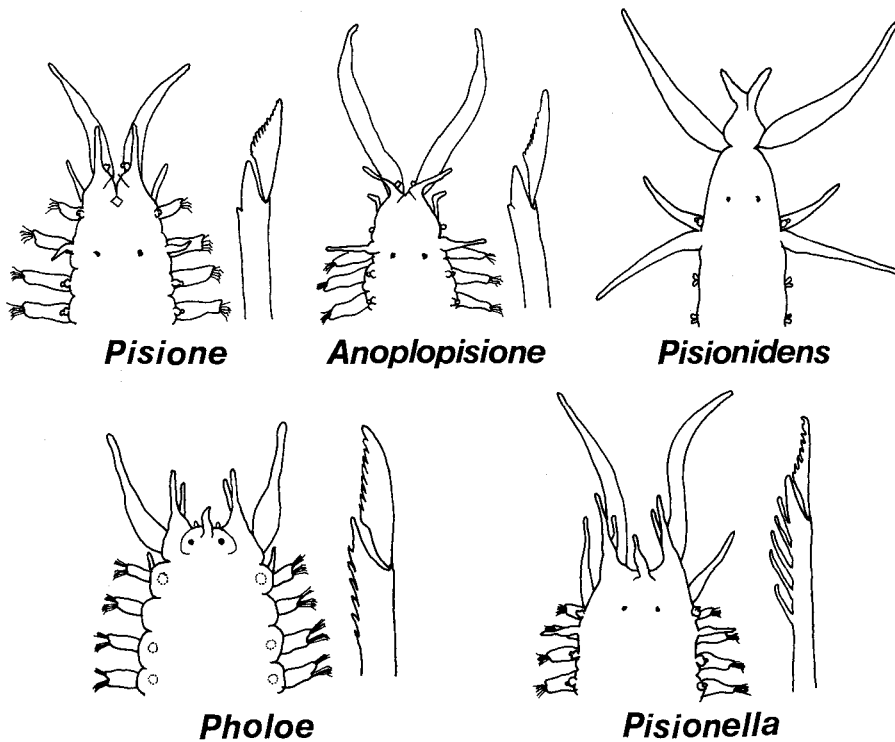


Fig. 21. Schematic representation of anterior end and falciger of *Pholoe* and the genera of the family Pisionidae.

discard such organs lest they should hinder the worms from locomotion. It is regarded as a case of retrogressive evolution in which such reduction has some adaptive significance (Swedmark, 1964). The seemingly random distribution of such morphological characters as the cephalic appendages and the setae shown in Table 10 can be explained as the results of the retrogressive evolution, because reduction of characters can take place in parallel among distantly related species.

Thus, it is more reasonable to consider that the characteristics peculiar to *Pisione* were once acquired by a larger, active burrower which proceeds pushing grains aside on locomotion and then reduced through retrogressive evolution into interstitial sliders in various ways, than to consider that they appeared separately among interstitial species. Then the ancestral form of *Pisione* is presumed to be a larger one with the appendages and the setae well-developed. This idea is supported by the existence of *P. mista* which is, in the genus, one of the largest species and fully keeps the characters specific to pisionids (Table 10). *Pisionella hancocki* Hartman, 1939, the only species of the genus which is most closely related to *Pholoe* as shown above, is also a large form. These large forms with more than 1 mm in body width excluding parapodia, should better be regarded as active burrowers than as interstitial sliders.

There is little correlation between body size and degree of reduction of these organs among the species of *Pisione*. Even in one of the largest species, *P. oerstedii*, the infra-acicular setae and the long bladed compound setae are absent. Large species with such reduced characters might have secondarily enlarged themselves after they have become interstitial

sliders, since chances to encounter habitats with larger dimensions are not rare for animals living in the interstice of sand grains.

Thus, evolutionary process in pisionids can be largely distinguished into two steps. As the first step, they have acquired and developed their unique characteristics in the course of the evolution from a *Pholoe*-like ancestor into active burrowers through colonization to sandy substrata without reducing their body size or organs: worms of this type may be represented by *Pisionella* and *Pisione mista*. Then, as the second step, retrogressive evolution into interstitial sliders has occurred among the species of *Pisione*, *Anoplopisione* and *Pisionidens*. It should be noted that *Pisionidens* may exhibit a good example of interstitial sliders comparable to *Polygordius*, a polychaete genus devoid of any traces of parapodia or setae. Though parapodia and setae show extreme reduction in *Pisionidens*, its trunk width is kept rather large (0.7 mm wide in *P. maturata* and about 0.5 mm wide in *P. indica*). In the course of the retrogressive evolution, species of *Pisionidens* are considered to have sacrificed their parapodia and setae hardly reducing their trunk width. Among the species of *Pisione*, the proportion of the length of parapodial stem to the trunk width (= body width excluding parapodia) of the same body segment rather increases with decrease of trunk width: in larger species with trunk widths more than 1 mm (*P. mista*, *P. oerstedii* and *P. pulla*), the proportion is about 1/3; in smaller species with trunk widths less than 0.2 mm (*P. brevicirra*, *P. martinsi*, *P. parhelenae* and *P. parva*), it is about 1/1; in other species of intermediate sizes, it is around 1/2. Thus, species of *Pisione* have not reduced the proportion of their parapodia to the trunk width in the course of the retrogressive evolution.

Adaptations in the reproductive biology is essential for interstitial polychaetes since they are not allowed to discharge a large number of gametes into free water as in the case of larger forms on account of the limited number of oocytes due to their small sizes. As has been summarized by Westheide (1984), they have created various devices to ensure fertilization of eggs (external fertilization by direct sperm transfer, hypodermic injection of sperms, true copulation, and hermaphroditism), and to reduce larval mortality (direct development of larvae, protection of eggs and brood, and vivipary). Pisionids are known to hatch out as trochophore larvae, hence no care of eggs or broods. They are considered to have settled the problem by producing a relatively large number of eggs for interstitial polychaetes (e.g. 600–800 per individual in *P. remota*, Stecher, 1968) on the one hand, and by achieving true, internal copulation (at least in *Pisione* and *Pisionidens*) on the other hand. Thus, species of *Pisione* have elaborated various copulatory devices which exhibit so highly complicated structure, especially in male copulatory apparatus, that their morphological characters are available not only for the classification of the species as shown in the present paper, but also in postulating the course of evolution in the genus.

Male copulatory apparatus and its phylogenetic significance:

Detailed examinations on male copulatory apparatus have been made on such species as *P. remota*, *P. gopalai*, *P. complexa*, *P. puzae*, *P. alikunhi*, *P. galapagoensis*, *P. crassa*, *P. hermansi*, *P. papuensis*, *P. helenae*, *P. parva*, *P. unguolata*, *P. brevicirra* and *P. hartmannschroederiae*. Among them, SEM has been efficiently used in examining the three-dimensional structures on the latter eight species. Efforts, however, were exclusively focused on the discrimination of individual species and no comprehensive comparative study on the apparatus has been attempted. The present study has newly revealed the structure of the apparatus of nine species or subspecies using SEM. Information on the male copulatory apparatus thus accumulated to the present makes it possible to arrange these species phylogenetically on the basis of their affinities.

Four groups of closely related species are recognized through comparison of male

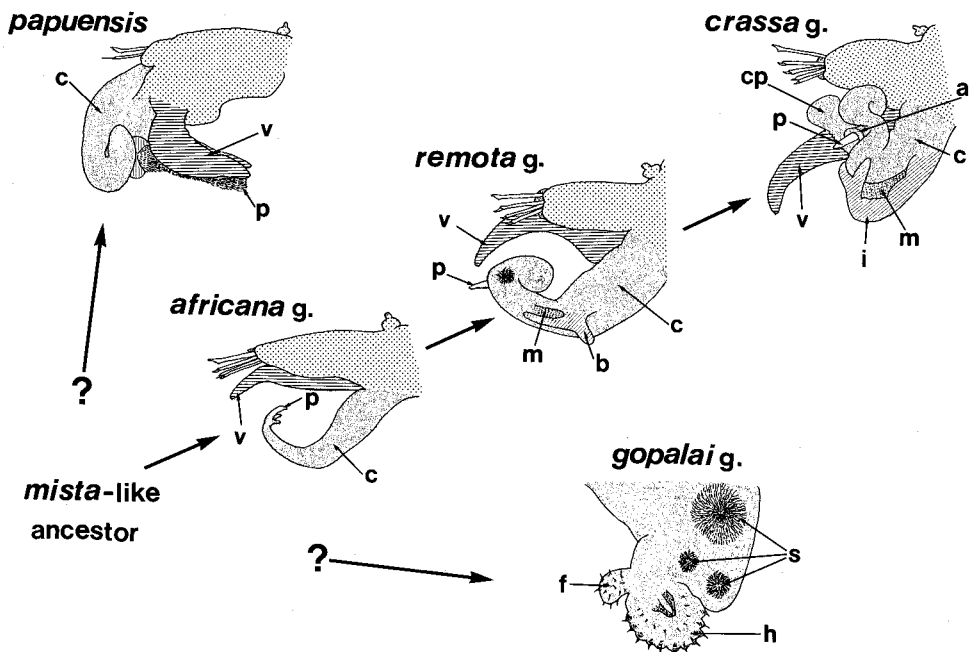


Fig. 22. Evolutionary trends in *Pisone* revealed through comparison of male copulatory apparatus. a: sheath-like arc, b: bidigitate process, c: copulatory organ proper, cp: cuticular plate, f: fan-like appendage, h: hood, i: inferior stem, m: cuticular membrane, p: penis, s: spinous papillae, v: ventral cirrus.

copulatory apparatus (Fig. 22). The first is represented by *P. crassa*, *P. hermansi* and *P. vestigialis* (*crassa* group). The stem of the copulatory organ proper is elongated so extensively as to form a thick, tapering structure. It twists to make up a spiral structure and ends in a cuticular penis. The ventral cirri of the segment are transformed into thick, finger-like processes with sensory hairs. A secondary, inferior stem of the copulatory organ arises from the ventral side of the main stem; they keep connection with each other by cuticular membrane; the inferior stem ends in a bidigitate process attached to the spiral part of the main stem. Around the penis such appendages as a sheath-like arc ("horse-shoe-shaped appendage" by Svonick, 1991) and an anterior cuticular plate ("golf club-shaped appendage and veil" by Svonick, 1991) are developed.

The second group is represented by *P. remota*, *P. puzae*, and *P. brevicirra* (*remota* group). Their copulatory organs are also elongate and show spiral structure with cuticularized penis; the ventral cirri are thick, finger-like processes. They are characterized by a bidigitate process arising from the ventral side of the main stem of the copulatory organ proper; it was named "t-förmiger Anhang" by Stecher (1968: Abb. 18) on *P. remota* and "appendice conica" on *P. remota* and *P. puzae* by Tenerelli (1965: Fig. 4,5 & 7). Intricate appendages are formed around the penis as in the case of the former group.

The third group is represented by *P. africana* and *P. unguata* (*africana* group). Their copulatory organ proper and ventral cirri of the segment are elongated as in the cases of the former two groups. But the shape of the copulatory organ is simple and not spirally wound; it is only provided with a subterminal digitate process.

In these three groups, parapodial lobes and setae remain unmodified or reduced only to a small extent. Segments with copulatory apparatus are located as a long series in

larger species, and reduce in number as body size decreases; in *P. brevicirra*, a small species, the apparatus are limited to a single segment.

The fourth group (*gopalai* group) is quite different from the former three. The copulatory organ proper and the parapodial stem are fused together to form a bulging structure. The ventral cirri and the setae are greatly reduced or entirely lost. Embedded acicula are well developed. Large masses of spinous papillae may be developed. A large hood with sensory hairs surrounds the protrusile penis. Copulatory apparatus of this type are usually located as a single pair, or separately if more than two on an individual, never on succeeding segments even in larger species. The representatives of this group are *P. gopalai* and *P. paucisetosa* which are closely related to each other only differing in the number of masses of spinous papillae. *P. parva* is considered to be allied to these species by the possession of the hood, though it lacks the spinous papillae and the fan-like appendage and the shape of copulatory apparatus is slender.

Though *P. papuensis* bears copulatory apparatus of bulging appearance, it possesses well-developed ventral cirri. So it cannot be related to the *gopalai* group.

Two evolutionary trends in the male copulatory apparatus are recognized in *Pisione* (Table 10 and Fig. 22). One is represented by the *crassa* group, the *remota* group and the *africana* group which are characterized by the elongation of the copulatory organ proper and of the ventral cirrus of the same segment. As mentioned above, the *crassa* group and the *remota* group are closely related in the spiral formation of the copulatory organ proper. In addition, the cuticular membrane connecting the outer digit of the bidigitate process and the main stem of copulatory organ in *P. remota* (Stecher, 1968) is considered to correspond to the membrane connecting the inferior and the main stem in the *crassa* group. This implies that the bidigitate process of the *remota* group and the inferior stem of the *crassa* group are homologous, and that the latter can be explained as a derivative of the former through elongation of the outer digit so extensively as to attach the lateral side of the spiral part of the main stem forming bifurcate ends. Therefore, the *crassa* group is considered to represent a more advanced condition in the elaboration of copulatory apparatus than the *remota* group. A more primitive condition in this trend is represented by the *africana* group; its copulatory organ is elongated with cuticular penis, but is not spirally wound and provided only by a minute digitate process subterminally; the ventral cirrus of the apparatus is elongated and the parapodial stem and the setae are unmodified as in the two groups. Thus, the species of *Pisione* characterized by the elongation of male copulatory organ proper and of the ventral cirrus can be arranged in the order of the *africana* group, the *remota* group, and the *crassa* group, from primitive to advanced.

The other trend is represented by the three species of the *gopalai* group which is characterized by the fusion of the copulatory organ proper and the parapodial stem with reducing ventral cirrus and setae. Among them, the male copulatory apparatus of *P. parva*, devoid of the spinous papillae and the fan-like appendage, is considered to represent a reduced condition on account of small size. More advanced or primitive condition in this trend has not been revealed among the known species.

Concerning other characters than male copulatory apparatus, each group shares some common characters (Table 10). In the *africana* group, the two species differ only in the notoacicula projecting through skin and in the presence or absence of infra-acicular simple setae. In the *remota* group, the dorsal cirri of 2nd setiger are short; the infra-acicular simple setae are present. In the *crassa* group, the prostomium is distinct; the inward projection of jaws are absent; the ventral cirri of 1st setiger are elongated; the presetal lobes are single. Both in the *remota* and the *crassa* groups, notoacicula do not project through the skin; the long-bladed compound setae absent. In the *gopalai* group, both the ventral

cirri of 1st setiger and the dorsal cirri of 2nd setiger are short; notoacacula do not project through the skin; the infra-acicular simple setae are absent. However, these characters are not restricted to any one of these groups. When species of the four groups are compared with each other in disregard of male copulatory apparatus, *P. remota* of the *remota* group and *P. vestigialis* of the *crassa* group should be regarded as most closely related, only differing in the shape of presetal lobes; in the same way, *P. brevicirra platycauda* of the *remota* group and *P. parva* of the *gopalai* group should be regarded as closely related, only differing in the presence or absence of the infra-acicular simple setae. It is thus evident that these groups cannot be defined by any other characters than male copulatory apparatus.

Along the supposed evolutionary order from the *africana* to the *crassa* group, some retrogressive trends are recognized in cephalic appendages and setae: in the *africana* group, most characters represented by *P. mista* are retained; in the *remota* and *crassa* groups, the long-bladed compound setae are entirely absent and the ventral cirri of 1st setiger and the dorsal cirri of 2nd setiger are reduced in many species; the infra-acicular simple setae are absent in two species of the *crassa* group. This trend agrees with the assumption that interstitial species of *Pisione* are derived from a larger one like *P. mista* through retrogressive evolution.

Although essential in the classification of polychaetes, the phylogenetic significance of such morphological characters as cephalic appendages, parapodia and setae are thus precluded in the genus *Pisione*. They are considered to be in retrogressive states due to interstitial life and cannot reveal true affinities among the species. On the other hand, the newly evolved characters characteristic of the group can be analyzed as representing apomorphic states and phylogenetic process. Copulatory devices of *Pisione* are considered to be secondarily developed in the course of adaptation for interstitial life in order to ensure fertilization of limited number of eggs. Their male copulatory apparatus composed of bulging gonadal pore and modified parapodial elements show high diversity among species with complex three-dimensional structures. Phylogenetic relationships of species level thus can be revealed in the genus *Pisione* through morphological analyses of male copulatory apparatus.

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Appendix

Key to the species of *Pisone* Grube, 1857

1. Dorsal cirri of 2nd setiger elongated; ventral cirri of 1st setiger longer than their parapodial lobe 2
 Dorsal cirri of 2nd setiger short and flask-shaped; ventral cirri of 1st setiger of various lengths 11
2. Dorsal cirri of 2nd setiger about twice as long as its parapodial lobe; prostomium distinct or indistinct 3
 Dorsal cirri of 2nd setiger nearly as long as its parapodial lobe; prostomium distinct 5
3. Long-bladed compound setae absent; prostomium indistinct; buccal acicula present; presetal lobes single; infra-acicular simple setae absent *P. oerstedii*
 Long-bladed compound setae present; presetal lobes bilobed 4
4. Prostomium distinct; buccal acicula present; infra-acicular simple setae present *P. mista*
 Prostomium indistinct; buccal acicula absent; infra-acicular simple setae absent *P. pulla*
5. Long-bladed compound setae present; buccal acicula projecting through the skin 6
 Long-bladed compound setae absent; presetal lobes single 10
6. Presetal lobes single 7
 Presetal lobes bilobed 8
7. Male copulatory organ spirally wound, partly fused to the parapodial stem *P. papuensis papuensis*
 Male copulatory organ straight with three distal appendages, not fused to the parapodial stem *P. hartmannschroederiae*
8. Notoacicula of median and posterior segments projecting through the skin *P. unguolata*
 Notoacicula embedded throughout the body 9
9. Male copulatory apparatus on a single segment; parapodial stem of the segment indistinct *P. papillata*
 Male copulatory apparatus on many succeeding segments; parapodial stem of the segments distinct and unmodified *P. africana*
10. Buccal acicula weak and entirely embedded *P. crassa*
 Buccal acicula strong projecting through the skin *P. hermansi*
11. Ventral cirri of 1st setiger equal to, or longer than their parapodial lobes; prostomium distinct; buccal acicula projecting through the skin 12
 Ventral cirri of 1st setiger shorter than their parapodial lobes 25
12. Infra-acicular simple setae present 13
 Infra-acicular simple setae absent 18
13. Long-bladed compound setae present; blade of lowermost falcigers smooth edged; presetal lobes single 14
 Long-bladed compound setae absent; blade of lowermost falcigers serrated 15
14. Notoacicula of median and posterior segments projecting through the skin *P. subulata*
 Notoacicula embedded throughout the body *P. levisetosa*
15. Palpi 4-5 times as long as dorsal cirri of buccal segments; presetal lobes single *P. longipalpa*
 Palpi about twice as long as those 16
16. Jaws with an inward projection; presetal lobes single *P. puzae*
 Jaws without inward projection 17
17. Presetal lobes bilobed anteriorly, single posteriorly; male copulatory organ single-stemmed *P. remota*
 Presetal lobes sub-bilobed throughout; male copulatory organ double-stemmed

- *P. vestigialis*
18. All the blades of compound setae more or less elongated *P. martinsi*
 Only the blade of uppermost compound seta elongated 19
19. Parapodial stem and setae of the segments with male copulatory apparatus unmodified;
 presetal lobes bilobed anteriorly, single posteriorly 20
 Parapodial lobe and setae of the segments with male copulatory apparatus modified ... 23
20. Male copulatory apparatus present on several succeeding segments; cuticular plate
 on the male copulatory organ 21
 Male copulatory apparatus on a single segment; without cuticular plate 22
21. Ventral cirri of the segments with male copulatory apparatus distally bifid
 *P. helenae*
 Ventral cirri of the segments with male copulatory apparatus distally unifid
 *P. umbraculifera*
22. Notoacacula of median and posterior segments projecting through the skin *P. primitiva*
 Notoacacula embedded throughout the body *P. bulbifera*
23. Ventral cirri of the segments with male copulatory apparatus branched; presetal lobes
 single *P. papuensis brevis*
 Ventral cirri of the segments with male copulatory apparatus unbranched 24
24. Ventral cirri of the segments with male copulatory apparatus with two subterminal
 appendages *P. galapagoensis*
 Ventral cirri of the segments with male copulatory apparatus without appendages
 *P. alikunhi*
25. Long-bladed compound setae present; infra-acicular simple setae absent 26
 Long-bladed compound setae absent; jaws with an inward projection; buccal acicula
 present; prostomium indistinct 33
26. Blade of long-bladed compound setae distally bidentate; buccal acicula present; jaws
 without inward projection; prostomium distinct 27
 Blade of longbladed compound setae distally unidentate 28
27. Presetal lobes single *P. laubieri*
 Presetal lobes bilobed *P. corallicola*
28. Buccal acicula absent; jaws with an inward projection; presetal lobes single; prostomium
 distinct *P. koepkei*
 Buccal acicula present; jaws without inward projection 29
29. Ventral cirri of the segments with male copulatory apparatus foliaceous; prostomium
 distinct *P. complexa*
 Ventral cirri of the segments with male copulatory apparatus entirely reduced, or
 fused to the copulatory organ 30
30. Pygidium with caudal organ; three falcigers on a parapodium 31
 Pygidium without caudal organ 32
31. Fan-like appendage present on the male copulatory organ; prostomium distinct
 *P. gopalai vannifera*
 Fan-like appendage absent; prostomium indistinct *P. gopalai gopalai*
32. Two falcigers on a parapodium; prostomium indistinct *P. paucisetosa*
 Three falcigers on a parapodium; prostomium distinct *P. parhelenae*
33. Infra-acicular simple setae present; male copulatory organ spirally wound near penis
 34
 Infra-acicular simple setae absent 35
34. Pygidium broad, semicircular; spinous pad present on the male copulatory organ
 *P. brevicirra platycauda*
 Pygidium normal; spinous pad absent *P. brevicirra brevicirra*
35. Presetal lobes bilobed anteriorly and single posteriorly; male copulatory apparatus
 provided with a hood *P. parva*
 Presetal lobes single; male copulatory apparatus unknown *P. reducta*

Explanation of Plates I-IV**Plate I**

Light microphotographs of entire worms.

1. *Pisione africana* Day, 1963. Male, Iv 1355, x 4.9.
2. *Pisione parva* De Wilde & Govaere, 1995. Male, Iv 1369, x 31.1.
3. *Pisione parva* De Wilde & Govaere, 1995. Female, Iv 1370, x 26.8.
4. *Pisione brevicirra platycauda* subsp. nov. Holotype. Male, Iv 1373, x 20.7.
5. *Pisione gopalai vannifera* subsp. nov. Holotype. Male, Iv 1379, x 8.6.
6. *Pisione papuensis brevis* subsp. nov. Holotype. Male, Iv 1384, x 7.6.
7. *Pisione bulbifera* sp. nov. Holotype. Male, Iv 1399, x 12.7.
8. *Pisione mista* sp. nov. Holotype. Male, Iv 1406, x 2.4.
9. *Pisione paucisetosa* sp. nov. Holotype. Male, Iv 1407; x 7.9.
10. *Pisione umbraculifera* sp. nov. Holotype. Male, Iv 1423; x 18.8.
11. *Pisione vestigialis* sp. nov. Holotype. Male, Iv 1427; x 5.1.

Plate II

SEM microphotographs of anterior ends.

1. *Pisione africana* Day, 1963. Dorsal view. Iv 1364, x 190.
2. *Pisione africana* Day, 1963. Ventral view. Iv 1364, x 135.
3. *Pisione parva* De Wilde & Govaere, 1995. Dorsal view. Iv 1371, x 302.
4. *Pisione parva* De Wilde & Govaere. Ventral view. Iv 1371, x 280.
5. *Pisione brevicirra platycauda* subsp. nov. Dorsal view. Iv 1377, x 219.
6. *Pisione brevicirra platycauda* subsp. nov. Ventral view. Iv 1377, x 258.
7. *Pisione gopalai vannifera* subsp. nov. Dorsal view. Iv 1383, x 190.
8. *Pisione papuensis brevis* subsp. nov. Dorsal view. Iv 1395, x 272.

Plate III

SEM microphotographs of anterior ends.

1. *Pisione bulbifera* sp. nov. Dorsal view. Iv 1405, x 188.
2. *Pisione bulbifera* sp. nov. Ventral view. Iv 1405, x 270.
3. *Pisione paucisetosa* sp. nov. Dorsal view. Iv 1420, x 177.
4. *Pisione paucisetosa* sp. nov. Ventral view. Iv 1420, x 117.
5. *Pisione umbraculifera* sp. nov. Dorsal view. Iv 1425, x 170.
6. *Pisione umbraculifera* sp. nov. Ventral view. Iv 1425, x 170.
7. *Pisione vestigialis* sp. nov. Dorsal view. Male, Iv 1440, x 275.
8. *Pisione vestigialis* sp. nov. Dorsal view. Female, Iv 1438, x 458.

Plate IV

SEM microphotographs of parapodia. t: terminal pores.

1. *Pisione africana* Day, 1963. Antero-dorsal view of a median parapodium. Iv 1364, x 338.
2. *Pisione parva* De Wilde & Govaere, 1995. Dorsal view of a median parapodium. Iv 1371, x 416.
3. *Pisione brevicirra platycauda* subsp. nov. Anterior view of a median parapodium. Iv 1377, x 562.
4. *Pisione gopalai vannifera* subsp. nov. Anterior view of an anterior parapodium. Iv 1383, x 1050.
5. *Pisione gopalai vannifera* subsp. nov. Anterior view of a median parapodium. Iv 1383, x 1036.
6. *Pisione papuensis brevis* subsp. nov. Anterior view of a median parapodium. Iv 1397, x 600.
7. *Pisione bulbifera* sp. nov. Anterior view of an anterior parapodium. Iv 1405, x 697.
8. *Pisione bulbifera* sp. nov. Anterior view of a median parapodium. Iv 1405, x 385.

Explanation of Plates V-VII

Plate V

SEM microphotographs of parapodia and posterior end.

1. *Pisone mista* sp. nov. Anterior view of a median parapodium. Iv 1406, x 136.
2. *Pisone paucisetosa* sp. nov. Anterior view of an anterior parapodium. Iv 1420, x 770.
3. *Pisone paucisetosa* sp. nov. Anterior view of a median parapodium. Iv 1420, x 795.
4. *Pisone umbraculifera* sp. nov. Anterior view of an anterior parapodium. Iv 1425, x 620.
5. *Pisone umbraculifera* sp. nov. Anterior view of a median parapodium. Iv 1425, x 392.
6. *Pisone vestigialis* sp. nov. Anterior view of a median parapodium. Iv 1440, x 363.
7. *Pisone gopalai vannifera* subsp. nov. Posterior end with caudal organ in ventral view. Iv 1383, x 250.
8. *Pisone gopalai vannifera* subsp. nov. Openings of caudal organ. Iv 1383, x 620.

Plate VI

SEM microphotographs of setae.

- 1-6. *Pisone africana* Day, 1963. Iv 1364, x 1790.
 1. supra-acicular simple seta; 2. long-bladed compound seta; 3. infra-acicular simple seta; 4. uppermost falciger; 5. median falciger; 6. lowermost falciger.
- 7-10. *Pisone parva* De Wilde & Govaere, 1995. Iv 1371, x 2170.
 7. supra-acicular simple seta; 8. uppermost falciger; 9. median falciger; 10. lowermost falciger.
- 11-14. *Pisone brevicirra platycauda* subsp. nov. Iv 1377, x 2440.
 11. supra-acicular simple seta; 12. infra-acicular simple seta; 13. upper falciger; 14. lower falciger.
- 15-19. *Pisone gopalai vannifera* subsp. nov. Iv 1383, x 2650.
 15. supra-acicular simple seta; 16. long-bladed compound seta; 17. uppermost falciger; 18. median falciger; 19. lowermost falciger.

Plate VII

SEM microphotographs of setae.

- 1-5. *Pisone papuensis brevis* subsp. nov. Iv 1396, x 1700.
 1. supra-acicular simple seta; 2. long-bladed compound seta; 3. uppermost falciger; 4. median falciger; 5. lowermost falciger.
- 6-10. *Pisone bulbifera* sp. nov. Iv 1405, x 2170.
 6. supra-acicular simple seta; 7. long-bladed compound seta; 8. uppermost falciger; 9. median falciger; 10. lowermost falciger.
- 11-15. *Pisone mista* sp. nov. Iv 1406.
 11. supra-acicular simple seta, x 530; 12. long-bladed compound seta, x 530; 13. uppermost falciger, x 1170; 14. median falciger, x 1170; 15. lowermost falciger, x 1170.

Explanation of Plates VIII-XI**Plate VIII**

SEM microphotographs of setae.

- 1-4. *Pisone paucisetosa* sp. nov. Iv 1420, x 1800.
 1. supra-acicular simple seta; 2. long-bladed compound seta; 3. upper falciger; 4. lower falciger.
- 5-9. *Pisone umbraculifera* sp. nov. Iv 1425, x 2230.
 5. supra-acicular simple seta; 6. long-bladed compound seta; 7. uppermost falciger, 8. median falciger; 9. lowermost falciger.
- 10-14. *Pisone vestigialis* sp. nov. male, Iv 1440, x 1700.
 10. supra-acicular simple seta; 11. infra-acicular simple seta; 12. uppermost falciger; 13. median falciger; 14. lowermost falciger.
- 15-18. *Pisone vestigialis* sp. nov. female, Iv 1438, x 1700.
 15. supra-acicular simple seta; 16. uppermost falciger; 17. upper-median falciger; 18. lowermost falciger.

Plate IX

SEM microphotographs of male copulatory organ: b: bidigitate process, h: hood, p: penis, sd: spinous pad.

- 1-2. *Pisone africana* Day, 1963. Iv 1364.
 1. ventro-lateral view, x 250; 2. penis, x 1470.
- 3-5. *Pisone parva* De Widle & Govaere, 1995. Iv 1372.
 3. ventral view x 229; 4. antero-lateral view, x 250; 5. terminal part, x 1440.
- 6-8. *Pisone brevicirra platycauda* subsp. nov. Iv 1378.
 6. ventral view, x 207; 7. inner lateral view, x 685; 8. outer lateral view, x 424.

Plate X

SEM microphotographs of male copulatory organ: c: copulatory organ proper; f: fan-like appendage; h: hood; k: knob; p: penis; sd: spinous pad; sp: spinous papillae; v: ventral cirrus.

- 1-2. *Pisone gopalai vannifera* subsp. nov. Iv 1383.
 1. ventral view, x 163; 2. inner lateral view, x 500.
- 3-4. *Pisone papuensis brevis* subsp. nov. Iv 1397.
 3. ventral view, x 136; 4. inner lateral view with penis protruded, x 273.
- 5-6. *Pisone bulbifera* sp. nov. Iv 1405.
 5. ventral view, x 158. 6. outer lateral view, x 583.
- 7-8. *Pisone paucisetosa* sp. nov. Iv 1421.
 7. ventral view, x 125; 8. inner lateral view, x 375.

Plate XI

SEM microphotographs of male copulatory organ: a: sheath-like arc; b: bulge in the center of spiral; cp: cuticular plate; d: digitate process; i: inferior stem; p: penis; s: superior stem.

- 1-3. *Pisone umbraculifera* sp. nov. Iv 1426.
 1. ventral view, x 310; 2. ventral view of terminal part, x 950; 3. subterminal appendage, x 1250.
- 4-6. *Pisone vestigialis* sp. nov. material not preserved.
 4. lateral view, x 250; 5. anterior view, x 500; 6. postero-lateral view, x 620.

